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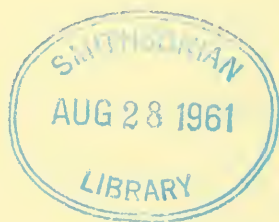


"EVERY MAN IS A VALUABLE MEMBER OF SOCIETY WHO, BY HIS OBSERVATIONS, RESEARCHES,
AND EXPERIMENTS, PROCURES KNOWLEDGE FOR MEN"—JAMES SMITHSON

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LEONARD CARMICHAEL,
Secretary, Smithsonian Institution.

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SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 140, NUMBER 1

CLASSIFICATION AND MULTIPLICITY
OF GROWTH LAYERS IN THE
BRANCHES OF TREES

AT THE EXTREME LOWER FOREST BORDER

(WITH 36 PLATES)

By

WALDO S. GLOCK

Macalester College, Saint Paul, Minn.

R. A. STUDHALTER

Texas Technological College, Lubbock, Tex.

AND

SHARLENE R. AGERTER

Macalester College, Saint Paul, Minn.



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TO
RALPH WORKS CHANEY

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(WITH 36 PLATES)

I. INTRODUCTION OBJECTIVES AND RESULTS

The work described in the following pages began as a desire to answer the apparently simple questions: When does a tree grow? How much does it grow? Where, on the plant body, does growth take place?

The objectives may be stated more formally in terms of cambial activity and maturation processes. These activities vary appreciably in time and space, and it is therefore pertinent to trace them in as much detail as possible with respect to diameter increase, formation of densewood, and tip elongation.

Results of observation, measurement, and experimentation have shown clearly that: (1) growth neither begins nor ends consistently at a certain time in all species, among all trees, among all branches, or over a single branch; (2) growth flushes may occur not only as annual but also as intra-annual cycles; (3) the amounts of xylem included in annual increments fluctuate, in general, over a relatively narrow range, whereas the amounts included in growth layers may fluctuate to an astonishing degree; (4) xylem may be formed as a

¹ Dr. Studhalter died on March 28, 1958.

sheath not only over all of a plant body during a single growth flush but also as a partial sheath over a large or very small portion of the plant; and (5) partial growth layers may be highly irregular in their distribution among different trees or over a single tree.

The present work has also shown clearly that: (1) cambial activity may either be general over a tree during the so-called growing season, or it may be highly localized in time as well as in space; (2) the rate and intensity of cambial activity may vary in time and in space; (3) the formation of densewood may be intermittent radially and tangentially; (4) the rate and intensity of densewood formation may vary in time and in space; and (5) the contact relations between densewood and lightwood may vary from abrupt alternation to complete transition.

After Glock had been using tree rings as a basis for chronologic and climatic interpretations for some years, it became increasingly apparent to him that the fundamentals of tree growth offered a more fruitful field of investigation. Therefore, the dynamic and biologic picture of tree growth to a large extent displaced in his mind the static picture of tree rings as purely mathematical entities.

Emphasis on the physiology and anatomy of tree growth quickly expanded the scope of investigation beyond the resources of one man. Soon after intensive work began, R. A. Studhalter was asked to take part in the expanded project because of his interest in the botanical aspects of growth-layer formation and because of his suggestions regarding artificial freezing of plant tissues.

ACKNOWLEDGMENTS

The work upon which the present report is based has received financial support by way of grants-in-aid from the Society of Sigma Xi, the Smithsonian Institution, and Texas Technological College. In January 1954 the National Science Foundation made a grant (Research Grant NSF-G610) with which to expedite and complete the project, and in August 1959 it made a further grant (NSF-G9539) toward publication of this paper.

D. L. Jones, superintendent of Substation No. 8, Texas Agricultural Experiment Station, at Lubbock, permitted us to experiment at length on many of the trees at the station. C. W. Van Horn, superintendent of Yuma Farms, University of Arizona Agricultural Experiment Station, sent us cuttings from citrus trees grown under irrigation.

To these organizations and persons we owe grateful acknowledgment for assistance and courtesies. Likewise, we are greatly indebted

to a large number of additional individuals who in one way or another contributed materially to the progress of our work.

Especially to Dr. I. W. Bailey do we owe a large measure of gratitude for demonstrating the anatomy of natural frost injury. The recognition of such injury along with its recovery actually formed the starting point of the present work.

Appreciation is expressed to Texas Technological College for the use of many facilities needed during the long period of time required for the completion of the work. Also appreciation is due Macalester College for use of similar facilities since 1948.

We are indebted to D. C. Dornberg of Saint Paul for many hours of careful work with the bulk of the photographs here included and to J. B. McBurney who prepared figures 34 and 35 and who generously assisted with the interpretative diagrams.

No detailed review of literature has been included in this report because several extensive reviews covering this subject have been published in the *Botanical Review* (Glock, 1941, 1955a; Studhalter, 1955).

II. THE TREES USED

LOCATION AND ENVIRONMENT

The plants used included both native and cultivated trees and shrubs. The great majority came from native species of trees planted on the campus of Texas Technological College or its immediate vicinity at Lubbock, Tex., where ecologic conditions are typical of the extreme lower forest border. However, comparisons were made with a natural forest-border area, with a systematically irrigated area, with an east-coast area, and with forest interiors. Natural forests occur below the Break of the Plains 35 to 55 miles east of Lubbock, in the mountains of New Mexico 260 miles northwestward, and in the Chisos Mountains 320 miles southward.

It is important to note that comparative studies revealed a close similarity between the growth-layer patterns of the planted trees at Lubbock and the patterns of the trees in the natural forests east of Lubbock.

LUBBOCK, TEXAS, AND VICINITY

This area supplied most of the trees for experimental purposes. The city of Lubbock lies in northwest Texas on the southern part of the High Plains at an elevation of 3,200 feet. On the whole, the

Plains are so flat that runoff in the area where the trees grew is at a minimum. The soil is a sandy chernosem of rather high porosity; it absorbs water and yields it to evaporation rapidly.

The climate of the area is typified by extremes of varying intensity. Annual rainfall averaged 19.09 inches over a period of 40 years. Table 1 gives certain rainfall data at the Texas Agricultural Experiment Substation, 5 miles east of the College campus. On the whole, rainfall is concentrated in the summer months, and therefore the trees may start growth in March or early in April with very little soil moisture available. The rains of spring and summer are commonly intense, of short duration, and separated by relatively long periods of drought. Because of the nature of the rainfall, soil moisture fluctuates widely.

Table 2 sets forth temperature data. Latitude causes a rather high average annual temperature, and altitude gives rather sharp fluctuations in daily and seasonal temperatures. Because of the rather high average annual temperature, growth begins rather early in the spring, sometimes as early as the first week of March, and temperatures which would permit growth continue late into autumn. However, this lateness is of little significance to tree growth except in certain instances where so-called postseasonal growth occurs.

The impact of a cold front during spring may delay initiation of growth or may force the temperature so low, after growth has started, as to kill or seriously injure the cambium and newly formed tissues. Temperature records permit us easily to identify the years of killing late frosts. The average date of the last killing frost in spring is April 14, and that of the first in autumn is November 1. Because of the highly unique character of the anatomical effects of a few of the late frosts, coupled with the knowledge of their exact dates, absolute dating of growth layers has been possible.

Table 3 sets forth data on evaporation and wind movement. It shows the relatively high rate of evaporation for all times of the year. There can be no doubt that a combination of high rate of evaporation, high temperatures in the summer, and long drought intervals, has detectable effects on tree growth.

The natural vegetation of the Lubbock area consists principally of short grass and widely scattered shrubby growth of catsclaw, yucca, and mesquite. Junipers are common at the Break of the Plains and in the transitional area immediately below. Locally, broad-leaved trees and shrubs are common in the canyons which fray the edge of the Plains.

The trees used for experimental purposes were either isolated in-

dividuals or members of windbreaks. In the latter case, however, competition could conceivably have accentuated somewhat, but not altered the nature of, the anatomical features in the xylem. This proved to be correct.

All trees used from the Lubbock area, with the exception of three, came from one of two places: the campus of Texas Technological College or the grounds of the Texas Agricultural Experiment Substation. Both places are very similar in being portions of nearly level areas. One of the other three trees grew in a shallow valley in MacKenzie State Park at the northeast edge of Lubbock; the second at a private residence in the west part of Lubbock; and the third in Coopers Canyon, a sharp valley heading into the Plains near Post, 40 miles southeast of Lubbock.

MOUNTAINS OF NORTHERN NEW MEXICO

This region was chosen partly because of accessibility and partly because of its native forest. Compared with the Lubbock region, the average annual rainfall is higher, the temperature lower, evaporation less, the soil moisture greater in amount and less in fluctuation, and the season of growth much shorter. These facts, coupled with the much greater elevation, make growing conditions less hazardous and more continuously favorable than in the Lubbock region.

A single ponderosa pine was sampled from the juniper-piñon-ponderosa pine association in the foothills near Las Vegas, N. Mex., at an elevation of 6,150 feet. Several trees and shrubs were sampled between Mora on the east slope and Tres Ritos on the west slope of the Sangre de Cristo Range at elevations ranging from 8,750 to 9,350 feet, elevations which put them well within the spruce-fir forest. The remaining New Mexico specimens came from stunted trees and shrubs at timberline near Serpent Lake above Tres Ritos at elevations ranging from 12,300 to 12,400 feet. Here the forest consists chiefly of Engelmann spruce, foxtail pine, and dwarf willow.

The timberline trees in New Mexico were under severe competition, but the others were not. Area rainfall is concentrated in the summer months, especially July and August, and averages 30 inches or more.

CHISOS MOUNTAINS OF SOUTHWEST TEXAS

This locality, in the Big Bend country, possesses environmental characteristics for all purposes strikingly intermediate between those of the New Mexico and the Lubbock regions. The trees came from

TABLE 1.—Monthly rainfall (in inches) at the Texas Agricultural Experiment Substation, Lubbock, Tex.

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
1911	.38	5.83	.43	2.36	.72	.28	6.75	.21	1.33	1.08	.22	1.55	21.14
1912	.02	1.28	.61	.50	1.58	.96	3.35	2.37	.73	2.81	.01	.38	14.60
1913	.04	.20	1.18	1.82	.24	5.88	.40	.32	4.19	1.53	1.54	2.12	19.46
1914	.15	.10	.31	1.46	4.04	3.86	6.17	5.95	.46	7.12	.35	1.47	31.44
1915	.09	3.00	2.52	6.18	1.52	4.01	1.42	2.96	7.86	1.52	.04	.76	31.88
1916	.17	T	1.15	2.63	.39	1.52	.36	2.45	2.79	2.91	.55	.11	15.03
1917	.35	.05	.21	.58	1.07	.64	1.42	1.16	3.03	.14	.08	T	8.73
1918	.84	.58	.05	.72	1.67	2.95	.53	.79	.79	.51	.69	2.33	12.45
1919	.12	.25	3.39	3.53	2.10	3.52	2.28	2.83	5.70	7.34	.36	.19	31.61
1920	.127	.11	.24	.15	2.91	3.66	2.19	2.64	1.63	1.43	2.22	.09	18.54
1921	.22	.45	1.47	.24	.43	7.71	.84	.92	4.50	.02	T	T	16.80
1922	.34	.20	.55	3.59	3.50	2.43	1.36	.28	.17	.56	1.50	.07	14.55
1923	.24	.86	1.04	3.18	2.77	3.98	1.65	1.59	2.67	6.80	.85	.64	26.27
1924	T	.17	.96	.86	.90	1.79	1.20	1.76	1.25	.47	.03	.15	9.54
1925	.65	.02	T	1.12	2.31	.86	3.38	3.32	9.44	1.33	.11	.21	22.75
1926	.56	.04	1.64	1.81	5.14	1.10	1.03	2.75	4.15	8.40	.67	1.63	28.92
1927	.79	.37	T	.40	T	2.91	2.16	.59	1.16	.40	T	.81	9.59
1928	.31	1.18	T	.15	3.08	1.06	6.78	4.04	.08	2.10	.74	.28	19.80
1929	.43	.34	2.03	.15	6.91	.90	.20	1.68	1.36	3.56	1.00	.07	18.63
1930	.61	.03	.45	1.04	1.71	1.70	.12	1.34	.11	3.91	.94	1.44	13.40
1931	.32	1.98	1.34	1.82	1.32	.95	2.17	2.44	.72	3.47	1.39	1.44	19.36
1932	.93	1.09	.04	1.84	2.37	5.66	1.90	3.15	3.41	1.29	T	2.48	24.16
1933	.37	.95	.02	.06	2.97	.21	1.36	2.19	.71	.42	.99	.06	10.31
1934	.06	.06	1.98	1.08	1.26	.28	.65	1.66	1.86	.28	.55	T	9.72
1935	.12	.60	.89	.04	3.49	2.57	1.25	1.69	3.02	1.22	2.04	.33	17.26
1936	1.08	T	.59	.92	5.86	.92	1.13	.13	13.93	1.52	.74	.21	27.03
1937	.26	.01	1.81	2.01	4.00	3.12	1.32	2.06	3.85	3.22	.07	.52	22.25

TABLE I.—Continued

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
1938	.91	1.18	.49	.14	1.99	5.89	4.01	.47	.63	.51	.27	.03	16.52
1939	.245	.19	.09	.28	1.82	.67	1.73	2.75	.01	.94	.18	.60	11.71
1940	.23	1.97	T	1.84	1.74	2.06	T	1.57	.73	1.07	2.35	.20	13.76
1941	.55	.61	3.56	2.23	12.69	4.13	3.68	1.85	4.47	5.89	.17	.72	40.55
1942	.04	.18	.51	3.25	.35	1.74	2.58	4.97	7.61	3.39	.01	2.70	27.33
1943	.04	.02	.25	.53	2.71	2.37	3.17	T	1.16	.10	.62	1.87	12.84
1944	1.28	1.36	1.09	.84	3.03	1.75	2.93	2.37	3.73	.80	1.72	1.64	22.54
1945	.69	.39	.10	.46	.46	.36	3.08	2.17	2.22	2.26	.27	.32	12.78
1946	.118	.15	.76	.07	1.49	2.72	.58	3.55	3.49	4.67	.44	1.04	20.14
1947	.73	.02	.69	1.06	6.35	1.56	1.06	.06	.08	.37	1.43	.52	13.93
1948	.14	1.38	.17	.33	2.88	2.31	1.75	.31	1.45	.98	.03	.13	11.86
1949	.405	.29	.80	1.84	7.80	4.05	1.18	2.07	4.76	1.49	T	.43	29.36
1950	.28	.18	T	.88	3.93	.68	3.12	2.08	3.74	.14	.03	.03	15.09
Mean	.58	.69	.84	1.35	2.79	2.41	2.05	1.94	2.87	2.20	.63	.74	19.09

T—means trace.

TABLE 2A.—Average monthly temperatures (in °F.) for the 5-year period 1936-1940, Lubbock, Tex.*

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
1936	38.8	40.8	55.4	59.9	69.2	78.6	80.0	80.6	70.1	58.2	47.6	44.7	60.3
1937	36.8	44.4	47.4	60.0	70.6	76.6	80.5	79.8	71.7	62.0	48.6	41.9	60.0
1938	43.6	48.2	56.0	60.4	70.6	75.8	77.8	79.2	73.0	64.8	48.8	43.0	61.8
1939	43.2	40.0	54.5	62.0	70.4	80.2	80.8	77.6	75.0	63.8	48.0	45.0	61.7
1940	34.0	44.6	54.8	61.4	69.3	75.0	82.6	77.8	73.6	63.8	48.3	44.5	60.8

* Data from United States Weather Bureau by courtesy of Houston, Tex., office.

TABLE 2B.—*Minimum and maximum daily temperatures (in °F.) for portions of 1938, Lubbock, Tex.*

Date	Min.	Max.	Date	Min.	Max.
Feb.			Apr.—continued		
20	26	45	3	32	73
21	19	36	4	39	87
22	25	53	5	51	85
23	27	52	6	42	78
24	34	46	7	24	43
25	26	53	8	23	41
26	32	59	9	23	67
27	33	63	10	35	78
28	47	63	11	42	75
Mar.			12	41	84
1	43	67	13	55	81
2	47	74	14	57	79
3	41	80	15	40	75
4	48	77	16	38	78
5	41	58	17	50	83
6	26	57	18	46	83
7	27	63	19	50	89
8	41	56	20	52	84
9	41	60	21	55	74
10	34	70	22	45	71
11	33	77	23	54	80
12	43	82	24	54	83
13	50	78	25	60	78
14	43	75	26	62	84
15	46	75	27	49	82
16	37	72	28	44	80
17	39	82	29	59	85
18	52	76	30	56	89
19	29	76	May		
20	42	84	1	65	91
21	52	83	2	56	91
22	44	78	3	66	87
23	31	67	4	51	78
24	37	85	5	50	81
25	51	89	6	48	88
26	35	77	7	41	83
27	34	43	8	31	70
28	39	64	9	44	67
29	44	73	10	47	74
30	40	75	11	48	87
31	31	63	12	53	83
Apr.			13	49	85
1	36	57	14	50	84
2	28	57	15	55	88
			16	65	90

TABLE 2B.—*Continued*

Date	Min.	Max.	Date	Min.	Max.
<i>May—continued</i>			<i>Oct.—continued</i>		
17	59	88	24	33	77
18	63	86	25	36	83
19	57	85	26	42	80
20	56	90	27	38	85
21	64	87	28	47	86
22	62	85	29	48	73
23	51	75	30	39	80
24	51	83	31	49	84
25	59	90	<i>Nov.</i>		
26	57	87	1	56	77
27	60	93	2	57	80
28	60	96	3	43	72
29	65	104	4	34	74
30	62	99	5	41	80
31	60	93	6	29	64
<i>Oct.</i>			7	20	45
1	53	89	8	23	61
2	52	90	9	26	65
3	50	90	10	38	79
4	54	93	11	42	80
5	52	88	12	48	81
6	55	83	13	49	71
7	55	79	14	39	78
8	53	80	15	30	79
9	59	77	16	47	78
10	54	73	17	49	80
11	59	74	18	37	64
12	62	88	19	25	72
13	49	88	20	26	70
14	53	88	21	27	73
15	53	85	22	19	46
16	53	83	23	15	35
17	48	84	24	7	51
18	48	87	25	21	50
19	53	75	26	13	48
20	38	65	27	12	52
21	38	80	28	16	56
22	52	69	29	23	65
23	32	58	30	19	74

TABLE 3A.—*Annual evaporation data (in inches) for the years 1931-1947 at Spur, Tex.*

Year	Evaporation
1931	64.171
1932	60.198
1933	72.753
1934	80.905
1935	64.272
1936	68.970
1937	64.657
1938	67.344
1939	73.157
1940	69.669
1941
1942
1943
1944	64.285
1945	63.015
1946	66.763
1947	63.408

TABLE 3C.—*Annual wind movement (by miles) for the years 1931-1947 at Spur, Tex.*

Year	Wind movement
1931	62,121
1932	53,739
1933	56,939
1934	69,582
1935
1936	63,709
1937	60,191
1938	62,003
1939	68,428
1940	70,585
1941	55,813
1942	55,226
1943	52,917
1944	38,830
1945	42,615
1946	66,562
1947	65,827

TABLE 3B.—*Monthly evaporation data (in inches) for the year 1938 at Spur, Tex.*

Month	Evaporation
January	3.051
February	2.131
March	5.627
April	5.177
May	8.057
June	7.641
July	7.082
August	9.003
September	6.898
October	5.581
November	4.006
December	3.090
Annual	67.344

TABLE 3D.—*Monthly wind movement (by miles) for the year 1938 at Spur, Tex.*

Month	Wind movement
January	5,082
February	5,135
March	7,670
April	7,144
May	6,536
June	5,391
July	3,838
August	3,757
September	3,288
October	3,604
November	5,694
December	4,864
Annual	62,003

the typical lower forest-border association of juniper-piñon at elevations of about 6,000 feet. Area rainfall is concentrated in the summer months, especially July and August.

YUMA, ARIZONA

The citrus trees, whose branches were sent to us, grew at the University of Arizona Experiment Station on a flat, mesalike area 4 miles south of Yuma. They were dependent almost wholly upon irrigation and therefore had an excellent opportunity of showing the effect of such irrigation on growth. The elevation of Yuma is 141 feet, and the Experiment Station is somewhat higher. Yuma has extremes of high temperature, low rainfall (annual average of 3.33 inches), and low soil moisture, so much so that plant life, except for the native desert association of creosote bush and cactuses, is absolutely dependent upon irrigation. The soil is light and very sandy. Competition was not a factor in the growth of the trees.

THE VICINITY OF WASHINGTON, D. C.

The trees used were planted and grew on the grounds of a private residence in Maryland, half a mile outside of the northwest boundary of the District of Columbia. They stood at an elevation of 230 feet on the slightly rolling surface of the Piedmont Plateau. The soil is a heavy clay loam.

The average annual rainfall of about 42 inches is much greater, and it is more evenly distributed, than that in the Lubbock region. Temperatures are in general somewhat lower and soil moisture fluctuations less; in spite of this, the trees suffered from drought effects while they were under daily observation. Killing frosts occur, and one was observed in the spring of 1944, one of the three springs during which the trees were under study. Cold spells in the spring periodically delayed growth. The specimen trees grew in an area where the mixed hardwood and pine forest had been cleared away. Competition did not affect any of them.

TREE DESCRIPTIONS

In order to refer to the specific locality and to a specific tree from that locality, the following symbols were adopted.

LOCALITY SYMBOLS

CC	Coopers Canyon near Post, Tex.
CM	Chisos Mountains, Tex.
Con	Conservatory, trees grown in, for one winter.
LV	Las Vegas, N. Mex.
M	Mackenzie Park, Lubbock, Tex.

S	Grounds of a private residence, Lubbock, Tex.
SL	Serpent Lake, above Tres Ritos, N. Mex.
TR	Tres Ritos, N. Mex.
TT	Texas Technological College campus, Lubbock.
W	Washington, D. C.
XS	Texas Agricultural Experiment Substation, Lubbock.
Y	University of Arizona Agricultural Experiment Station, Yuma.

SPECIES SYMBOLS

A	<i>Hibiscus syriacus</i> , shrubalthea, rose-of-Sharon.
Al	<i>Alnus tenuifolia</i> , thinleaf alder.
Ap	<i>Malus sylvestris</i> (<i>Pyrus malus</i>), apple.
As	<i>Fraxinus</i> sp., ash.
Asp	<i>Populus tremuloides</i> , quaking aspen.
C	<i>Cupressus arizonica</i> , Arizona cypress.
Cb	<i>Sapindus drummondii</i> , wild chinaberry, soapberry.
Ch	<i>Prunus</i> sp., black cherry.
Ct	<i>Citrus maxima</i> (<i>C. grandis</i>), grapefruit.
Cw	<i>Populus</i> sp., cottonwood.
E	<i>Ulmus pumila</i> , Siberian elm (often misalled Chinese elm).
F	<i>Abies lasiocarpa</i> var. <i>arizonica</i> , corkbark fir; <i>A. concolor</i> , white fir.
Fl	<i>Pinus flexilis</i> , limber pine.
G	<i>Grossularia</i> sp., gooseberry.
J	<i>Juniperus flaccida</i> , drooping juniper; <i>J. pachyphloea</i> , alligator juniper; <i>J. sibirica</i> , dwarf juniper; <i>J. virginiana</i> , red cedar; <i>Juniperus</i> sp., red cedar.
Jf	<i>Pinus jeffreyi</i> , Jeffrey pine.
L	<i>Gleditsia triacanthos</i> , honeylocust.
M	<i>Acer saccharinum</i> , silver maple.
O	<i>Elaeagnus angustifolia</i> , Russian olive, oleaster.
P	<i>Pinus aristata</i> , foxtail pine, bristlecone pine; <i>P. cembroides</i> , Mexican piñon; <i>P. ponderosa</i> , ponderosa pine; <i>Pinus</i> sp.
Pe	<i>Prunus persica</i> (<i>Amygdalus persica</i>), peach.
Pl	<i>Prunus</i> sp., plum.
S	<i>Platanus occidentalis</i> , American sycamore.
Sp	<i>Picea engelmannii</i> , Engelmann spruce.
T	<i>Pinus taeda</i> , loblolly pine.
Th	<i>Thuja</i> sp., arborvitae.
V	<i>Vitex agnus-castus</i> , vitex, chaste or hemp tree.
W	<i>Salix</i> spp., willow.

The complete symbol used to designate each single tree or shrub was made by combining a locality symbol with a species symbol. For instance, a pine from the campus of Texas Technological College was designated TTP, for Texas Technological pine, and a wild chinaberry from Coopers Canyon was, after a similar fashion, labeled CCCb.

Information having to do with the trees used in our work is given in table 4 and includes complete symbol, specific name, height, diameter, amount of competition, and certain additional ecological data. Diameter is given under symbol D.b.h., diameter breast high.

TABLE 4.—Detailed descriptions of experimental trees

Symbol	Name	Height feet	D.b.h. inches	Competition	Remarks
Gymnosperms					
CMJ 1	<i>Juniperus pachyphloea</i>	15	5	none	Note 1.* Slope steep, N-facing; elev. 5,900 ft.; soil rocky; drainage good.
CMJ 2	<i>Juniperus flaccida</i>	10	3	none	Slope steep, NE-facing; elev. 6,000 ft.; soil rocky; drainage good.
CMP 1	<i>Pinus cembroides</i>	12	2½	slight	Slope steep, NE-facing; elev. 5,900 ft.; soil rocky; drainage good.
Con C 1	<i>Cupressus arizonica</i>	2±		none	Just out of seedling stage.
Con P 1	<i>Pinus ponderosa</i>	2		none	Note 2. In bushy stage; no tip growth in conservatory.
Con P 2	<i>Pinus ponderosa</i>	1		none	Slow growing.
Con T 1	<i>Pinus taeda</i>	5	1½	slight	Grew rather rapidly after transplanting.
Con T 2	<i>Pinus taeda</i>	5½	1½	slight	Same as preceding. Note 3.
Con T 3	<i>Pinus taeda</i>	5	1½	none	Frozen so severely by artificial means as to be dead by May 1940.
LVP 1	<i>Pinus ponderosa</i>	25	7½	none	Slope gentle, W-facing; elev. 6,150 ft.; soil rocky.
MP 1	<i>Pinus</i> sp.	12	5	none	Foot of gentle slope, N-facing, 10 ft. above valley bottom. Note 4.
SLJ 1	<i>Juniperus sibirica</i>	1½		none	Shrubby; slope steep, E-facing; elev. 12,300 ft.; soil rocky.
SLP 1	<i>Pinus aristata</i>	3		none	Shrubby; slope steep, E-facing; elev. 12,300 ft.; soil rocky and dry.

* See Notes to Table, p. 19. (Continued)

TABLE 4.—Continued

Symbol	Name	Height feet	D.b.h. inches	Competition	Remarks
SLSp 1	<i>Picea engelmannii</i>	2		none	Shrubby; slope steep, SE-facing; elev. 12,400 ft.; soil rocky and dry.
TRF 1	<i>Abies lasiocarpa</i> var. <i>arizonica</i>	30	6	none	Slope gentle, NE-facing; elev. 9,350 ft.; soil deep and well drained.
TRF 2	<i>Abies concolor</i>	30	6	none	Same as preceding.
TRF 3	<i>Abies lasiocarpa</i> var. <i>arizonica</i>	30	6	severe	Moist meadow; elev. 9,000 ft.
TRF1 1	<i>Pinus flexilis</i>	20	5	none	Slope gentle, SE-facing; 15 ft. above meadow; elev. 9,300 ft.; soil thin, not constantly wet.
TRJ 1	<i>Juniperus sibirica</i>	2		none	Shrubby; slope gentle, at edge of meadow; elev. 9,300 ft.; soil rocky and dry.
TRP 1	<i>Pinus aristata</i>	20	16	none	Slope steep, SW-facing; elev. 9,000 ft.; soil rocky and dry.
TRP 2	<i>Pinus ponderosa</i>	50	15	none	Slope steep, SW-facing; elev. 8,750 ft.; soil moist, rich, slightly rocky.
TRSp 1	<i>Picea engelmannii</i>	27	7	moderate	Slope gentle; elev. 8,900 ft.; soil deep.
TRSp 2	<i>Picea engelmannii</i>	25	6	slight	Slope gentle, NE-facing; elev. 8,800 ft.; soil rocky and dry.
TTC 1	<i>Cupressus arizonica</i>	20	4½	none	Note 5. Stands 10 ft. away from a low building.
TTC 2	<i>Cupressus arizonica</i>	37	8	moderate	In a sheltered corner on south side of large building; irrigated.

(Continued)

TABLE 4.—Continued

Symbol	Name	Height feet	D.b.h. inches	Competition	Remarks
TTC 5	<i>Cupressus arizonica</i>	16	5	none	11 branches sectioned.
TTC 12	<i>Cupressus arizonica</i>	8	4	severe	Both trunk and branches sectioned.
TTC 30	<i>Cupressus arizonica</i>	20	7	none	Watered throughout growing seasons.
TTC 31	<i>Cupressus arizonica</i>	20	11 $\frac{3}{4}$	very slight	Bushy; 13 stems from ground level.
TTC 32	<i>Cupressus arizonica</i>	24	1 $\frac{1}{2}$ -3 $\frac{1}{2}$	very slight	Plowed twice yearly; 20 branches sectioned.
TTC 33	<i>Cupressus arizonica</i>	16	10	none	30 branches sectioned.
TTC 34	<i>Cupressus arizonica</i>	21	11	none	Multiple stems.
TTC 35	<i>Cupressus arizonica</i>	19	11 $\frac{1}{2}$	none	Multiple stems.
TTC 36	<i>Cupressus arizonica</i>	31	13	none	Multiple stems.
TTC 37	<i>Cupressus arizonica</i>	16	12	none	Multiple stems.
TTJ 1	<i>Juniperus virginiana</i>	11	4	severe	18 branches sectioned.
TTJ 2	<i>Juniperus virginiana</i>	13	5	slight	
TTJ 3	<i>Juniperus sp.</i>	14	5 $\frac{1}{2}$	severe	
TTJ 4	<i>Juniperus virginiana</i>	17	11	moderate	
TTJ 5	<i>Juniperus virginiana</i>	15	4	none	Multiple trunk from soil level, one trunk dominant.
TTP 20	<i>Pinus ponderosa</i>	15	5	none	43 branches sectioned.
TTP 21	<i>Pinus ponderosa</i>	15	4 $\frac{1}{2}$	none	
TTP 22	<i>Pinus sp.</i>	20 $\frac{1}{2}$	5 $\frac{1}{2}$	none	Slow growing; branches numerous; needles sparse.
TTP 23	<i>Pinus ponderosa</i>	14	6	none	Vigorous and heavily branched; 20 branches sectioned.
TTP 24	<i>Pinus ponderosa</i>	17	5	none	Vigorous, many branches and heavily needled; 25 branches sectioned.
TTTh 1	<i>Thuja sp.</i>	9		moderate	Multiple stem from ground level; irrigated.

(Continued)

TABLE 4.—Continued

Symbol	Name	Height feet	D.b.h. inches	Competition	Remarks
TTTh 2	<i>Thuja</i> sp.	35	8	moderate	In a sheltered corner on south side of a large building; irrigated. Note 6.
XSC 1	<i>Cupressus arizonica</i>	26	9	slight	A bushy clump of 5 stems. A bushy clump of 6 stems. Diameter at ground level. A bushy clump of 10 stems. A bushy clump of 5 stems. Two main stems with branches at and above ground.
XSC 2	<i>Cupressus arizonica</i>	26	10	slight	
XSC 3	<i>Cupressus arizonica</i>	26	10½	slight	
XSC 4	<i>Cupressus arizonica</i>	26	8½	slight	
XSC 6	<i>Cupressus arizonica</i>	26	11	slight	
XSC 8	<i>Cupressus arizonica</i>	13	3-4	moderate	A native tree in its native habitat; on a bench away from creek. Bushy, of many stems; irrigated frequently; pruned periodically. Same remarks as preceding. On irrigated lawn and partially surrounded by concrete.
XSC 9	<i>Cupressus arizonica</i>	16	4	moderate	
XSC 10	<i>Cupressus arizonica</i>	14	12	moderate	
XSC 11	<i>Cupressus arizonica</i>	16	3-3½	moderate	
XSC 12	<i>Cupressus arizonica</i>	19	to 5	moderate	
XSC 13	<i>Cupressus arizonica</i>	17	3½	moderate	
XSJf 1	<i>Pinus jeffreyi</i>	14	6	severe	A native tree in its native habitat; on a bench away from creek. Bushy, of many stems; irrigated frequently; pruned periodically. Same remarks as preceding. On irrigated lawn and partially surrounded by concrete.
XSJf 2	<i>Pinus jeffreyi</i>	16	6	severe	
XSP 1	<i>Pinus ponderosa</i>	26	8½	severe	
XSP 2	<i>Pinus ponderosa</i>	22	9	severe	
Dicotyledons					
CCCb 1	<i>Sapindus drummondii</i>	18	19	slight	
SA 5	<i>Hibiscus syriacus</i>	10		moderate	
SA 6	<i>Hibiscus syriacus</i>	9		moderate	
SE 1	<i>Ulmus pumila</i>	27	10	moderate	

(Continued)

TABLE 4.—Continued

Symbol	Name	Height feet	D.b.h. inches	Competition	Remarks
SLG 1	<i>Grossularia</i> sp.	2		moderate	Slope steep, SE-facing; elev. 12,400 ft.; soil rocky and dry.
SLW 1	<i>Salix</i> sp.	2		severe	Slope steep, S-facing; elev. 12,400 ft.; soil rocky and dry.
SLW 2	<i>Salix</i> , another sp.	2½		severe	Same as preceding.
TRAI 1	<i>Alnus tenuifolia</i>	20	5	moderate	Slope gentle, NW-facing; elev. 8,800 ft.; soil semi-marshy.
TRAsp 1	<i>Populus tremuloides</i>	?	5	slight	Slope gentle, NE-facing; edge of dry alpine meadow; elev. 8,900 ft.
TRG 1	<i>Grossularia</i> sp.	4		moderate	Level; elev. 8,800 ft.; soil semi-marshy; near stream.
TRW 1	<i>Salix</i> sp.	10	1½	slight	Slope gentle; NW-facing; elev. 8,800 ft.; soil semi-marshy.
TRW 2	<i>Salix</i> sp.	9	1	none	Slope steep, NW-facing; elev. 8,800 ft.; soil rocky; near edge of stream.
TTAp 1	<i>Malus sylvestris</i>	11	7¼	none	Note 5. No irrigation at time samples were growing.
TTAp 2	<i>Malus sylvestris</i>	10½	9	none	Heavy irrigation during year previous to taking sample.
TTAs 1	<i>Fraxinus</i> sp.	26	3¾	slight	On a lawn; watered frequently.
TTcW 1	<i>Populus</i> sp.	30	5½	none	Same remarks as preceding; 17 branches sectioned.

(Continued)

TABLE 4.—Continued

Symbol	Name	Height feet	D.b.h. inches	Competition	Remarks
TTE 1	<i>Ulmus pumila</i>	28	12	slight	Note 7, 10 branches sectioned.
TTE 2	<i>Ulmus pumila</i>	15	4	severe	
TTE 3	<i>Ulmus pumila</i>	7	$\frac{1}{2}$	severe	
TTE 4	<i>Ulmus pumila</i>	12	2	severe	
TTE 5	<i>Ulmus pumila</i>	9	$\frac{3}{4}$	severe	
TTL 1	<i>Gleditsia triacanthos</i>	18	6	moderate	Sparsely branched. All honeylocusts grew in windbreaks.
TTL 2	<i>Gleditsia triacanthos</i>	12	4	severe	
TTL 3	<i>Gleditsia triacanthos</i>	14	5	moderate	9 branches sectioned.
TTL 4	<i>Gleditsia triacanthos</i>	15	6	severe	
TTL 5	<i>Gleditsia triacanthos</i>	17	6-9	severe	9 branches sectioned; diameter varies on different radii.
TTM 1	<i>Acer saccharinum</i>	18	6 $\frac{1}{2}$	slight	On watered lawn; 11 branches sectioned.
TTM 3	<i>Acer saccharinum</i>	20	8	slight	On watered lawn.
TTO 1	<i>Elaeagnus angustifolia</i>	15	10 $\frac{1}{2}$	slight	On watered lawn near paved street.
TTS 1	<i>Platanus occidentalis</i>	15	6	none	Near paved street; soil much trampled.
TTV 1	<i>Vitex agnus-castus</i>	9		moderate	Bushy; against south wall of building.
WAp 1	<i>Malus sylvestris</i>	6	1 $\frac{1}{2}$	none	Wettest location of Washington trees; on bottom of grassed-over drainage way.
WCh 1	<i>Prunus</i> sp.	8	1 $\frac{1}{2}$	none	Slope gentle, NW-facing.
WCh 2	<i>Prunus</i> sp.	8 $\frac{1}{2}$	2	none	Down slope from preceding.
WCh 3	<i>Prunus</i> sp.	6	1	none	Farther down slope.

(Continued)

TABLE 4.—*Concluded*

Symbol	Name	Height feet	D.b.h. inches	Competition	Remarks
WPe 1	<i>Prunus persica</i>	5½	1	none	On crest of slope above WCh 1.
WP1 1	<i>Prunus</i> sp.	6½	1	none	Down slope from WPe 1.
YCt 1	<i>Citrus maxima</i>			none	Note 8.
YCt 2	<i>Citrus maxima</i>			none	
YCt 3	<i>Citrus maxima</i>			none	
YCt 4	<i>Citrus maxima</i>			none	

Notes to Table 4

1 (CMJ 1).—Diameter taken at 4½ feet above the ground designated d.b.h., except in cases of multiple trunks, where the measurements were taken closer to the ground level.

2 (Con C 1).—All trees labeled Con were moved to the Conservatory of the Biology Department of Texas Technological College from the Texas Agricultural Experiment Substation on November 16, 1939. On April 24, 1940, the trees then alive were transplanted to the grounds of a residence in west Lubbock, where they were partially shaded by larger trees and were irrigated periodically in connection with a lawn.

3 (Con T 2).—Trunk subjected to severe artificial freezing in three places, April 1940; all foliage killed; tip growth 2.7 feet from April 1940 to May 1944, when entire tree was sectioned.

4 (MP 1).—This tree, as well as the others of the Lubbock area, was under observation or subjected to experimentation during a period which included 1941, the year of the highest rainfall on record in Lubbock. More than half the year's total rainfall occurred during the two months of April and May, the time when the greatest amount of tree growth was made.

5 (TTC 1).—All experimental trees growing on the campus of the College grew under conditions of little or no drainage to

or from the trees. Insofar as the work was concerned, competition for a great majority of the trees was nonexistent. They grew in a nearly natural vegetational environment with the exception of a few isolated cases in windbreaks, lawns, or an orchard, noted under "Remarks."

6 (XSC 1).—The trees from Texas Agricultural Experiment Substation grew in isolated north-south windbreaks. Only branches which grew in full sunlight were used in experimental work. Isolated instances of irrigation shortened the waterless intervals and built up soil moisture, which decreased markedly between rains, even during 1941, the wettest year on record.

7 (TTE 1).—Because the terminal buds of the twigs of *Ulmus* commonly die and therefore force new tip growths to emerge from lateral buds, the trees of this genus offer difficulties in tip growth and dating measurements.

8 (YCt 1 to 4).—These came from cuttings not necessarily from the same tree for any one number; No. 1 included 14 cuttings 1 year old; No. 2 included 16 cuttings 2 years old; No. 3 included 7 cuttings 3 years old; and No. 4 included 2 cuttings 4 years old.

III. THE METHODS USED

The work that forms the basis of the present report was done from 1939 to 1950 upon complete sections cut from the branches of trees or shrubs, except for eight trunks which were dissected in whole or in part.

Both macroscopic and microscopic methods were used, the former including for the most part labeling, observations, measurements, and artificial freezing, and the latter the preparation and analysis of microtome sections. In actual detailed experimentation and measurement more branches were always chosen than would ordinarily be necessary in order to allow for damage by man, ice storms, and incidental hazards. Exploratory samples were taken from diverse trees in diverse habitats for the purpose of comparing them with the trees from which the majority of the specimens was taken. With the exception of those methods devised for special purposes in the development of our work, the remainder were, of course, those common to botanical and silvicultural practices.

All experiments, observations, measurements, and thin-section analyses were made by Glock and Studhalter working together at the same time. This joint work holds true except for the years 1942 to 1945, when each one carried on independently work applicable to the common problem.

MACROSCOPIC METHODS

Simple descriptions based on locality were sufficient in the Lubbock area to maintain the identity of individual trees. With branches, however, it was quite different. Their identity was maintained in two ways: first, by a band of twine at an appropriate place; and second, by close measurement from the ground up the trunk and out the branch, especially from significant crotch to crotch, until the exact place of measurement or experimentation was reached. With these details recorded, we found it possible to return to an exact spot on a particular branch at any time.

Each tree was given a letter symbol and a number, as has previously been explained. Branches used from any one tree were numbered consecutively. For instance, TTP 20-43 refers to Texas Technological College pine tree Number 20 and to the 43d branch selected therefrom. When a branch was removed for dissection, blocks were cut at intervals throughout its length, the innermost being labeled *a*, and those successively outward, *b*, *c*, and the like. The final designation of a block reads, therefore, as follows: TTP 20-43-a. If a hand

or macroscopic block was preserved from the immediate vicinity of the *a* block, it was given the designation A.

Measurements made on tip growth of branches were taken either weekly or annually. The weekly records were made throughout the entire warm season or else over a calendar year. Annual measurements were carried on for a minimum of one year to a maximum of four years. In addition to these more or less periodic measurements, the amount of tip growth was customarily recorded whenever any experimental work was performed. The purpose of the tip-growth measurements was not primarily to determine the amount of such growth, but actually to determine the relationship between the number of tip flushes and the number of diameter flushes, and the relative amounts of each.

As an extension of tip-growth measurements, phenologic observations were carried on, in some cases daily, in others weekly. These were made not only on trees which were later sampled, but also on the general woody vegetation of the area. The phenomena observed included the start of tip elongation, leafing out, development of cones and flowers, progress of different types of growth, branching, setting of buds, resumption of tip growth, and pest attacks. Also, information was gathered on late frosts, temperature fluctuations, and rainfall.

Branches frozen artificially (Studhalter and Glock, 1942) received an injury which, together with recovery therefrom, later appeared in the xylem and could be used as a reference to relate the injury to the exact time of growth-layer formation. In addition to such "internal tagging," artificial freezing yielded information on the nature of frost injury and the recovery of living tissue from the effects of different intensities of injury.

When observation and experimentation had been completed on any branches, they were removed from the trees, and blocks were cut from them. The actual time of removal depended upon the purpose the experiments were intended to serve. Many, of course, were taken during the winter which is supposedly the season of least growth. In this way, postseasonal growth could be detected. Those blocks taken at various times during the growing season permitted us to identify multiple diameter flushes. In several instances, a series of similar branches was removed from the tree, one being taken every two weeks. In connection with the freezing experiments, many different branches on a tree were artificially frozen at one time; they were then removed one at a time at successively longer intervals in order to determine the

time and amount of diameter growth, as well as to observe regeneration of living tissues.

In November 1939 nine trees (three ponderosa pines, three loblolly pines, and three Arizona cypresses) were moved from the grounds of the Texas Agricultural Experiment Substation to large cans in the Conservatory of Texas Technological College. In April 1940 they were transplanted to the grounds of a private residence a half mile from the College campus. These trees were kept under constant observation and measurement until the last of them was cut down and dissected in May 1944.

Increment cores were not used in our work. In fact, our methods were designed especially to avoid their use because it was learned early in the work that a core, as one radius, is wholly inadequate to give a picture of the growth-layer pattern throughout a trunk or branch under extreme lower forest-border conditions.

MICROSCOPIC METHODS

In all cases, branches were cut from the trees by means of a fine-toothed coping saw. Blocks suitable for immediate sectioning with a microtome, or for storage in a formalin-acetic-alcohol fixing agent for future sectioning with a microtome, were removed from the branches in the laboratory with the same saw. Wherever possible, a set of two blocks was taken from each locality on a branch so that both cross and longitudinal sections could be made. The number of branches removed from an individual tree varied from 1 to 43, dependent upon the purposes of the experiments. The number of blocks taken from a single branch varied from 1 to 17, counting only the blocks taken for cross sections.

In the entire project, a total of 433 branches and 5 main trunks were brought to the laboratory. As a matter of passing interest, we may mention that 1,245 blocks were taken from these branches and trunks for the purpose of cutting cross sections, and 553 blocks were also taken, from which both radial and tangential sections were cut.

A table microtome, used during the early part of the project, was soon superseded by a sliding microtome. The thickness of the sections varied with the type, size, and condition of the materials and averaged about 30 microns. All staining was done with safranin and fast green. Counting cross, radial, and tangential sections, slides totaled some 2,500 in number; however, for the purposes of the present report, we concentrated on cross-section slides from 1,500 blocks.

The wood blocks were ordinarily not softened before sectioning

with the microtome. It was often necessary to determine whether the cambium was alive or active at the time of taking the specimen, as in freezing experiments; and in the determination of the time of beginning and of cessation of cambial activity, it was important that the cambium cells be left as nearly normal as fixing and staining techniques would permit. For these reasons, sections were cut either from freshly sawed blocks, or else the latter were fixed in formalin-acetic-alcohol and sectioned later with no additional treatment.

All sections were examined under low-low (21X), low (60X), and high (264X) powers. In those cases where it was possible, sections were examined closely prior to staining, either under a wide-field binocular (13.8X) or under a hand lens (14X). A comparison of the results achieved with the unstained sections on the one hand and the stained sections on the other, brought out vividly and emphatically the great advantage of stained over unstained sections. Many cases of uncertainty on unstained sections were resolved quickly and accurately when the sections had been stained.

IV. ABSOLUTE DATING—CRITERIA OF MULTIPLICITY

DISCOVERY OF PRECISE DATING

In late 1938, Glock began the study of stained sections from branches of trees growing on the campus of Texas Technological College and noted a severe frost injury and recovery zone in the inner portion of the outermost growth layer (Glock and Reed, 1940; Glock, 1951). It was soon determined that the injury was due to a severe frost early in April 1938, which almost universally damaged the vegetation of the area.

In February 1939 realization came that, with proper use as taught and described by Bailey (1925), late spring frosts could be employed as a method of precise dating of the annual increments of xylem because the time of occurrence of the frost was known with exactness. This method of dating opened up the possibilities of extended investigation which was, nevertheless, distinctly limited by dependence upon the natural frosts which came with irregular frequency and intensity.

While Glock was engaged in the task of dating annual increments and their included growth layers by means of natural frost, Studhalter, in May 1939, conceived the idea of devising a method of producing an injury in branches by means of frost artificially induced by dry ice (Studhalter and Glock, 1942). He suggested to Glock that artificial frost might supplement the effects of natural frost and as a

result joined Glock in October 1939 in an attack on problems opened up by the development of methods of precise dating. Thus the work has dealt with dated annual increments and in many cases with growth layers dated to a part of a growing season.

The development of the two methods of absolute dating, by the use of natural and artificial frosts as time markers in the detection of annual increments, led directly to the search for, and development of, other possible methods or criteria.

It was realized at once that a third method consisted of carefully observing and measuring tip growth over a period of a year or more and then of cutting sections from the measured portion of the tip growth.

As a fourth method, a discrepancy between the number of tip flushes and the number of diameter flushes suggests multiplicity. For instance, if two diameter flushes are incorporated in one tip flush, the evidence is presumptive for more than one diameter flush for the particular growing season. A discrepancy of this kind, we have found, is an entirely different type of evidence compared with the existence of one diameter flush to two tip flushes, a duality far from rare in the forest-border area in one season.

The fifth method to be used in the detection of multiplicity—comparison of structural features—is rather weak and has been used only as corroborative evidence; growth layers of comparable width, similar sequences of growth layers, and the matching of special features such as a widespread injury are suggestive, but by no means conclusive, time markers.

These five methods, or criteria, are the bases upon which the entire study has been elaborated. They will be taken up in further detail.

METHODS OF ABSOLUTE DATING

NATURAL FROST EFFECTS

By the term "frost" we mean both frost injury and recovery; by the term "natural frost" we mean especially late (spring) frost, unless otherwise stated. The typical natural frosts, which stand out prominently in the Lubbock area and have been used almost exclusively in absolute dating, are those of 1938, 1936, and 1934, in that order of usefulness. For most of the work, in which natural frost served to give absolute dating, that of 1938 proved to be the most typical, the most uniform in occurrence, and the most readily identifiable (pls. 8; 19, fig. 2; 20; 24, fig. 1; 29; 33).

The original correlation of each frost with its correct year was

based upon extensive sampling at the end of the 1938 growth period, upon sampling of trees growing under conditions of constantly available soil moisture, and upon a combination of meteorological and phenological records and observations. A combination of all of them left no doubt as to the identity, characteristics, and intensity of the typical frosts enumerated above. Moreover, the fact that the temperature of 1935 did not drop below freezing in the Lubbock area after the middle of February eliminates all possibility of the existence of frost injury in the xylem grown in 1935. A knowledge of this absence serves as a check interior to 1936 whereas the time of first sampling, the winter of 1938-1939, placed a limit exterior to the 1938 growth layer.

In many of the sections studied, the following typical sequence served as an anchor for extension into other parts of the same branch, other branches, other trees, and other species:

1934 annual increment, with moderately intense frost effects.

1935 annual increment, in which frost effects are impossible.

1936 annual increment, with moderately intense frost effects.

1937 annual increment, with light frost effects showing commonly as spots.

1938 annual increment, with intense frost effects.

Early work in dating depended upon the presence of the characteristic 1938 frost effects in the outer part of our sections, whereas later work attempted to reach back to include 1938 frost effects in the inner part of the sections and to reach forward to tie in with the 1945 frost effects, which will permit us to extend the work into the future, with precise dating assured. Recent fieldwork indicates that the frost injury of 1945 will be as much of a key to absolute dating as was that of 1938.

The entire sequence, as well as each unit of the sequence, served as an absolute check in precise dating. These checks controlled the dating and established multiplicity wherever it occurred. In some cases, where there was a question as to the date of different frost effects because of certain atypical occurrences among them, the fact that the 1935 increment could not possibly contain a frost acted as a control in the dating of the increments both preceding and following it. The correct combination of frost effects in different years had to include a 1935 increment which was free of those effects.

The presence of frost effects depends, of course, upon the intensity of the climatic factor, upon the species concerned, and upon the condition of growth at the time of the frost. If the frost was intense, as for instance in 1938, and if the meristematic tissues were active, very few species in the Lubbock area escaped the effects. The silver maple was

one such to escape; in contrast, the Siberian elm was severely ruptured in the cambial region down to the ground, even in trunks 8 inches in diameter.

In detail, there is much variation among species, even for the intense 1938 frost. This is strikingly true of the Arizona cypress and the several species of yellow pines. Other frosts, of less intensity, show greater variation among different species.

Among different trees of the same species and among different branches of the same tree, the variations in frost effects duplicate in a large measure what has been said above about species. The case is somewhat different in relation to occurrence in branches; here, the outer 5 to 30 cm. were unaffected by frost. The extent of the frost effects inward on the branch is extremely variable, and most of our sections did not reach inward far enough to reveal their lower limit.

Where a frost effect is typically developed, it has a characteristic intensity, a characteristic extent around the circuit, and a characteristic position in the xylem near, or at the beginning of, the annual increment. The frost effects for 1934, for instance, do not commonly extend around the circuit; they lie either flush against the densewood of the preceding growth layer, or else out one or two cells. In contrast, the effects of the 1936 frost commonly extend around the circuit and lie nearly flush against the densewood of the preceding growth layer. If the effects are not continuous around the circuit, the localized occurrence lies in that part of the increment having the greatest thickness; in other words, in that region where cambial activity was initiated sufficiently early so that it was caught by the frost. The effects for 1937 are always highly localized as spots which, in many cases, appear to be sunk in the densewood of the first growth layer of the 1937 annual increment. The frost effects for 1938, the most typical and easily recognizable of all, extend completely around the circuit in the majority of instances and are located in the xylem some distance out from the start of the season's growth, a matter of two or three and up to six or eight cells. Further study will bring out the essential characteristics of the 1945 frost; however, those effects for the years 1939 to 1944, although better known than those for 1945, are less dependable because of greater variation in position, extent, and occurrence. The annual increments for 1932 and 1933 also contain frost effects as a characteristic, but so few of our sections contain these increments that it was not possible for us to become as intimately acquainted with them as with the 1934-to-1938 sequence. The sporadic frosts, those of 1937, 1939, 1940, 1941, and 1944, have high value for dating purposes when present because they check off the

beginning of their respective annual increments, especially where they are multiple.

A striking feature of a few branches was the occurrence of the effects of two frosts in the 1938 increment. The initial effects, feeble, inconspicuous, and commonly restricted to the two cusps of lenses, involved the very first cells set off when diameter growth began in the spring. The second or later frost produced the effects of the typical 1938 frost. In a rare instance or two, there was a third injury and recovery resembling those of frost; however, we cannot be certain of such an identification. Where present, the double frost effects can be used in dating.

ARTIFICIAL FROST

Artificial frost injury and recovery resemble their natural counterparts in all respects. Our experiments were confined to the branches of Arizona cypresses, yellow pines, and junipers on the campus of Texas Technological College and the grounds of the Texas Agricultural Experiment Substation near Lubbock (pls. 2, figs. 1 and 2; 23, fig. 2; 24).

The original purpose of artificial freezing was to place an internal tag in the nature of an injury and recovery within the xylem before it matured. By a series of calibration experiments, it was intended to determine the time and intensity of application necessary to produce identifiable results. If this could be done (and it was), it would give immediately a method of placing an internal tag at any desired time in relation to diameter growth and at any desired place in the woody framework of a tree. Excellent results, as a matter of fact, were obtained in those cases where the cambium and cambial derivatives were in the proper state to receive and record the shock of freezing; however, the proportion of successful internal tagging experiments was low in relation to the total number carried out.

Internal tagging was unsuccessful under two circumstances: the freezing was applied too late in the growing season, or it was too intense to permit subsequent recovery. In the climate of the Lubbock region, it was found that artificial freezing should be applied before the middle of April in order to strike the cambium in the condition most susceptible to frost injury. Growth here begins anywhere between March 1 and April 1, and may be well along in the first flush of diameter growth by the middle of April.

As a matter of fact, even though experiments in internal tagging were not carried through in the numbers to be desired, the anatomical

results were so striking as to be ample remuneration for the work entailed. These results will be detailed in succeeding chapters. In addition to the purely anatomical results so far achieved, the method of artificial freezing has a wide field of application in dating precisely the time of formation of annual, as well as intra-annual, growth layers. Furthermore, the method can be extended from small branches, such as we have used, to limbs and to trunks of trees that are too large to lend themselves to tip-growth measurements or to the effects of natural frosts.

TIP-GROWTH MEASUREMENTS

These measurements, in some cases weekly, in others yearly, were used as a third means for the absolute dating of the diameter flushes within that part of the branch which had grown during the measurements. The existence of two or more growth layers in the tip growth measured for one year gave clear proof of multiplicity. Correct locations on the branches were maintained by the methods described previously and gave certainty even in those instances where bud scale scars were not developed. In the case of yearly measurements, they were made during the winter for one to several years. Weekly or periodic measurements were begun well before the start of the growing season and were terminated at least a year later. Obviously, sections taken from the branch tip grown during the measured intervals could contain only the diameter flushes grown during the same intervals.

Annual measurements of tip growth were made on the following species in the Lubbock area: *Conifers*—ponderosa pine (4 trees, 81 branches), loblolly pine (2 trees, 35 branches), a short-leaved yellow pine (MP 1; 1 tree, 3 branches), another short-leaved pine (TTP 22; 1 tree, 7 branches), Arizona cypress (6 trees, 36 branches), and red cedar (3 trees, 11 branches). *Dicotyledons*—apple (2 trees, 5 branches), cottonwood (1 tree, 7 branches), Siberian elm (1 tree, 6 branches), honeylocust (3 trees, 15 branches), and silver maple (2 trees, 12 branches). At Washington, D. C., annual measurements were made on the following species of young fruit trees: Apple (1 tree, 2 branches), cherry (2 trees, 8 branches), peach (1 tree, 11 branches), and plum (1 tree, 2 branches). Through the kindness of Mr. Van Horn, we were able to obtain grapefruit cuttings from Yuma, Ariz., which represented the tip growth for specific years; these included 15 branches probably from four different trees. The total of annual measurements thus included 256 branches from 35

trees of 16 different species. Of this total, 16 branches were measured at weekly intervals for a full year or more.

The method of sustained periodic measurements (weekly in the main) was applied to the following coniferous species in the Lubbock area: Ponderosa pine (1 tree, 5 branches), loblolly pine (2 trees, 4 branches), a short-leaved yellow pine (TTP 22; 1 tree, 1 branch), Arizona cypress (2 trees, 4 branches), and red cedar (2 trees, 2 branches). At Washington, D. C., periodic measurements were made on the following species of young fruit trees: Apple (1 tree, 1 branch), cherry (3 trees, 9 branches), peach (1 tree, 6 branches), and plum (1 tree, 3 branches). Thus the total of sustained periodic measurements included 35 branches on 14 trees of 9 different species. Within this total, there occurred 17 cases in which annual measurements of one to three years preceded or followed a year of periodic (weekly) measurements.

Because of the nature of observations and the taking of specimens, many cases developed where it was possible to secure accurate measurements of tip growth for intervals varying from approximately a week to a full growing season. These short-interval measurements were made on the following species in the Lubbock area: *Conifers*—ponderosa pine (6 trees, 26 branches), loblolly pine (2 trees, 12 branches), Jeffrey pine (2 trees, 4 branches), a short-leaved yellow pine (MP 1; 1 tree, 1 branch), another short-leaved yellow pine (TTP 22; 1 tree, 2 branches), Arizona cypress (8 trees, 55 branches), and red cedar (3 trees, 14 branches). *Dicotyledons*—apple (3 trees, 14 branches), ash (1 tree, 1 branch), Siberian elm (1 tree, 2 branches), cottonwood (1 tree, 3 branches), honeylocust (4 trees, 8 branches), silver maple (2 trees, 10 branches), sycamore (1 tree, 1 branch), and vitex (1 tree, 1 branch). In the mountains of northern New Mexico, the following species were measured for short-interval tip growth: *Conifers*—foxtail pine (1 tree, 1 branch), corkbark fir (1 tree, 1 branch), and Engelmann spruce (1 tree, 1 branch). *Dicotyledons*—gooseberry (1 shrub, 1 branch). At Washington, D. C., the following species were measured in the same manner: Apple (1 tree, 1 branch), cherry (3 trees, 9 branches), peach (1 tree, 15 branches), and plum (1 tree, 2 branches). The total of all short-interval measurements, therefore, included 185 branches from 47 trees of 23 different species. Of this total, there were 137 cases of short-interval measurements on branches which were in turn measured annually for an interval of one to four years.

In addition to actual measurements made either annually or periodically, a third method of obtaining tip-growth increments em-

ployed the presence of terminal bud scale scars counted inward on the branch. This method in itself is not considered universally accurate in setting off increments of annual increase in length, a fact to be elaborated under the chapter on multiplicity. In truth, it was found that a disparity between the number of tip flushes and the number of diameter flushes in many cases provided a key to multiplicity of growth flushes within one year.

Terminal bud scale scars were used in two ways: first, where the internodes were actually measured; and second, where they were merely counted.

The following species in the Lubbock area came under the first heading, actual measurements: *Conifers*—ponderosa pine (4 trees, 15 branches), loblolly pine (2 trees, 3 branches), and a short-leaved yellow pine (MP 1; 1 tree, 1 branch). *Dicotyledons*—apple (3 trees, 14 branches), ash (1 tree, 1 branch), cottonwood (1 tree, 2 branches), honeylocust (3 trees, 6 branches), silver maple (2 trees, 7 branches), sycamore (1 tree, 1 branch), and vitex (1 tree, 2 branches). These totaled 52 branches from 19 trees of 10 different species. Under the second heading for the Lubbock area, terminal bud scale scars were counted, with total measurement to the sections taken but no measurement on individual internodes, on the following species: *Conifers*—ponderosa pine (4 trees, 19 branches). *Dicotyledons*—Siberian elm (2 trees, 6 branches), cottonwood (1 tree, 1 branch), honeylocust (2 trees, 2 branches), and silver maple (1 tree, 1 branch).

The second type of use of terminal bud scale scars, counting only, included the following species from northern New Mexico: *Conifers*—ponderosa pine (2 trees, 2 branches), foxtail pine (2 trees, 2 branches), limber pine (1 tree, 1 branch), corkbark fir (2 trees, 2 branches), white fir (1 tree, 1 branch), and Englemann spruce (3 trees, 3 branches). *Dicotyledons*—alder (1 tree, 1 branch), aspen (1 tree, 1 branch), gooseberry (2 bushes, 2 branches), and willow (4 trees, 4 branches). The total of counted terminal bud scale scars came to 48 branches from 29 trees of 20 different species.

As a matter of passing interest, a grand total of tip-growth measurements was made upon 576 branches from 72 different trees distributed among 12 coniferous and 17 dicotyledonous species.

The data on tip growth so far described have depended upon accurate measurements at either regular or irregular time intervals. In addition to such measurements, many direct and sustained observations were made—observations made at intervals which ranged all the way from daily to several weeks. These observations were of three types: First, close observations of the branches immediately

surrounding a measured branch and comparison with the latter, as well as general observations on the entire tree in comparison with the same single branch; second, short-interval, close observations of individual branches, information on which was recorded by successive diagrams and by notes; and third, general observations on the conditions of the vegetation from the beginning of leafing out and initiation of tip growth until the following winter.

In some respects, observations as described above give a better picture of what a tree as a whole is doing than measurements of a single branch; this is especially true of the relationship among different branches and among different trees as regards initiation of growth, decrease in growth rate, actual intraseasonal halts, and the final setting of winter buds.

It is clear, of course, that growth layers formed in tip flushes which have been measured periodically are thereby dated with exactness. These growth layers can be followed inward on the branch by means of a series of sections.

NUMBER OF DIAMETER FLUSHES IN RELATION TO NUMBER OF TIP FLUSHES

At once three possibilities become obvious, namely: (1) The number of diameter flushes equals the number of tip flushes, (2) the number of diameter flushes exceeds the number of tip flushes, and (3) the number of diameter flushes falls short of the number of tip flushes.

The first case represents very probably the normal situation, wherein a single diameter flush corresponds to each tip flush. If the single tip flush constitutes a single year's growth and extends from the terminal bud scale scars at the base of a former terminal bud to the bud scale scars at the base of the next outer terminal bud, then the corresponding diameter flush is an annual growth layer. If the actual dates of formation of tip-growth increments are unknown, we make no presumption of multiplicity in a one-to-one correspondence of diameter and tip flushes.

The second case is held to be clear proof of multiplicity because the maximum length of time involved in the formation of one tip flush is one full growing season. Two diameter flushes in a single tip flush represent the minimum amount of multiplicity over an annual interval. Should tip flushes themselves be multiple within a year, the multiplicity of growth layers is correspondingly increased.

The third case probably requires more than one tip flush in a season and does not necessarily concern the problems of multiplicity.

Certain problems and concepts having to do with tip flushes and their transitional forms, as well as the relation to actual tip flushes of multiple zones on a branch, each zone composed of a bare portion and a needle-covered portion, will be considered later in the chapter on multiplicity.

In view of the generally accepted fact that one tip flush can represent no more than a single year of growth, the existence of two growth layers in one tip flush is acceptable evidence for multiplicity.

Further discussion of the relationships between diameter flushes and tip flushes will be given later (pages 183-204).

CORRELATION OF STRUCTURAL FEATURES

Within the same branch, and even within the same tree, special features such as width of growth layer, similar sequence, characteristic "doubles," circles of parenchyma cells, or injury other than frost could be used occasionally to help identify growth layers from section to section as an extension of absolute dating. No great reliance was placed upon these features.

For instance, an injury in the growth layer for 1936 in several of the Arizona cypresses persisted farther out along the branches than did the known natural frosts by which the growth layer was dated. Another example of marked assistance was an annual increment consisting of two sharply bounded growth layers, the inner one wide and the outer very narrow. This "double" proved especially characteristic and helpful for 1937, 1939, and 1940 among Arizona cypresses and junipers. As in the case of all structural features, the "double" was first dated on an absolute standard before it was used in a secondary role.

Growth-layer width by itself, as seen in cross section, was of little correlative value. However, relative width of adjacent growth layers did offer assistance when based initially on absolute dating.

SUMMARY STATEMENT

The problem of the unity or multiplicity of growth layers in one year has been discussed more or less emphatically from time to time by different workers. Evidence for unity has been cited from one region, whereas evidence for multiplicity has been announced from another. If precision methods, or absolute dating, could be applied over a region, the uncertainty would be eliminated.

Absolute dating was made possible by the recognition of the effects of the 1938 natural frost in the Lubbock region. This same

frost was recognized and verified in the Chisos Mountains, 320 miles south of Lubbock. Later, other methods supplemented and extended the possibilities of absolute dating. It should be emphasized that this type of dating contrasts sharply with those methods dependent upon counting or upon the presence of one checkpoint in many years. By means of natural frost, artificial frost, or measured tip growth, the growth layers of each branch used in this work have been dated exactly.

Absolute dating gives a great advantage in this type of work and permits a breadth of application not heretofore realized. By this means we should readily be able to detect multiplicity of growth layers in a rather marked lower forest-border region as represented by the Lubbock area. However, before the rather involved topic of multiplicity is considered, it will be well to examine all types of growth layers and to determine if they can be classified structurally or genetically. This can lead us to a rational definition of a growth layer—rational from the physiological point of view.

V. CLASSIFICATION OF GROWTH LAYERS

INTRODUCTION

Classification is a necessary, initial step in an intensive investigation of growth layers. Early studies indicated that certain growth layers may be disposed over the plant body in a somewhat complex fashion. In attempting to describe the variety of growth layers encountered, we adopted a terminology that seemed suitable and suggestive.

A consideration of growth layers from an anatomical point of view and an appreciation of cambial activity from the physiological point of view depend to a great extent upon the mental picture of a growth layer as it exists within the body of a tree. In addition, this picture possesses ecologic implications. The older idea, and the one largely current today, is that of rings which are concentric circles as seen on the end of a log or the top of a stump. Hence, the popular term "tree rings" is used rather than "growth layers," and the simplicity of a two-dimensional concept contrasts with the anatomical correctness of the three-dimensional concept. The principles of physiology, anatomy, and ecology leave no alternative but to consider tree growth a complex process resulting in a three-dimensional growth layer more or less intricately disposed over the body of a tree.

In the construction of a terminology, the terms must be highly descriptive; they must conform to the three-dimensional picture even though they are derived from the cross-sectional appearance of the

growth layers. The terms "locally absent" (Douglass, 1935, p. 68) and "locally present" (Glock, 1937, pp. 8-9), for instance, are loosely descriptive because they lack clear-cut definition and originated in an intensive study of rings on cross sections, whereas "lens" not only gives a definite picture but also is inherently a three-dimensional affair. In other words, a lens is at once visualized as a patch of xylem on the body of a tree.

Even greater difficulties are brought into focus by the use of such negative terms as "occasionally absent," "commonly absent," or "missing ring" (Douglass, 1935, pp. 58-72), because these depend wholly upon one radius or at most one cross section from each tree. Elsewhere along the body of a tree the situation may be decidedly different. It may be illustrated as follows: A certain "ring" is entire around the circuit on one cross section of a tree; another cross section shows the same "ring" to be locally present; and a third section shows it to be absent or missing. Of course, a ring is missing only in the sense that it was never formed. Attention cannot thus be centered too exclusively on a two-dimensional viewpoint, or be concentrated on a single radius or cross section from each tree. The term "lens," on the contrary, includes all three of the above concepts and necessarily prohibits the concentration of attention on a single plane in the body of a tree.

A problem worthy of investigation arises from the designation "missing ring." Can a growth layer, present entirely or partially in one tree, be completely absent from the body of another tree? Ecological physiology says "yes" if the growth layer is an intra-annual. However, the problem becomes acute if the growth layer actually or supposedly represents one full year of growth. Such absence would signify physiological activity sufficient only to keep the meristematic tissues alive, but insufficient, over an interval exceeding a year, to permit cell division and maturation at any time during that interval. The problem is too complicated and far-reaching to be settled here. A first step would be to establish without doubt the annual character of the growth layer which tends to be partially or entirely absent. The present paper, it is hoped, is a step forward in the solution of this problem.

Of course, designating a growth layer as locally absent, commonly absent, or missing on a single radius or section does not mean that the worker considers it to be the same throughout the entire body of the tree. The use of such terminology may eventually restrict his viewpoint. Genuine harm, however, would come from the actual substitution of an unduly small linear dimension for a volume quantity,

no matter how truthfully the ratio of thicknesses of adjacent growth layers represents their volume ratio where the growth layers are sheaths surrounding the entire plant body. Any single linear measurement of a partial growth layer from zero up to the maximum thickness would thus in all probability enter statistical calculations or graphic analyses as either a plus or minus exaggeration.

The nomenclature used in the classification of growth layers has developed gradually during the course of the work. As has been mentioned heretofore, almost all growth layers have been studied on a series of cross sections taken along each branch. An attempt has been made to adopt a terminology that will instantly describe the appearance of the growth layer on a cross section, at the same time suggesting its three-dimensional nature. Consistent with such usage, a growth layer is thick or thin, in radial dimension, rather than wide or narrow (Glock, 1937, p. 73).

CONSTITUENTS OF A GROWTH LAYER

TERMS

Our knowledge of furniture, woodwork, and lumber of all kinds has familiarized us with the common pattern of alternating light and dark bands in wood. This same alternation is shown on a log or on any surface cut transversely to the length of the trunk. As is well known, each pair, a light plus a dark band, forms a so-called tree ring, or growth layer. The common idea of a tree ring pictures it as beginning abruptly with light-colored wood which passes outward gradually into darker material whose outer termination comes abruptly. This succession is repeated in each ring. However, the more one studies not only rings on a cross section but also growth layers along a branch or trunk, the more complex their anatomy becomes.

So far as the gross constituents of a growth layer are concerned, different points of view may stress time of formation, position in the growth layer, or structure of the tissues. The two parts of a growth layer have been given different names, such as: (1) springwood and autumnwood, (2) springwood and summerwood, (3) earlywood and latewood, or (4) lightwood and densewood. The first three stress *time of formation*, a valuable distinction if there is uniformity among trees and if time is distributed correctly. Observation and experimentation throw doubt on the strict validity of both suppositions. In the case of springwood and autumnwood no comment need be added, but with springwood and summerwood any objections seem trivial until one wonders whether spring is an astronomic or a climatic

designation. The only serious ambiguity arises in case of multiple growth layers in a year. Should we use springwood and summerwood in relation to an outer growth layer formed, say in July, or late in the *growing* season, whatever portion of the calendar this may span? At first sight, earlywood and latewood, based upon mutual relationship in time, seem to be more accurate and more justifiably descriptive than previous terms. We have, however, found latewood present at the beginning of a growth layer, and we have seen it within the body of an annual increment as fragments, intermittent circles, and complete circles preceding the latest earlywood of the increment. Surely, latewood should be later than earlywood.

Terminology based upon *position in the growth layer* has not been proposed, apparently, in a formal manner. "Inner part" and "outer part" have been used descriptively (Holman and Robbins, 1939, p. 117). These are rather weak and subject to the same indefiniteness as those previously mentioned. In the same category are the terms "red ring" and "red autumn ring" (Douglass, 1928, p. 32).

The third basis for discriminating between parts of a growth layer, *structure of the tissues*, is committed neither to time of formation nor to relative position within the growth layer or annual increment. *Lightwood* and *densewood* are thus terms descriptive of the cellular nature of the tissues. It seems worthy of note that, although botanical workers have stressed xylem structure, they have commonly made use of a nomenclature based on time. However that may be, a structural term is eminently descriptive and can be applied to any type of growth layer no matter when formed or how completely formed. The terms for the two general types of xylem in growth layers, "light" and "dense," have only structural and textural implications.

The structural characteristics involved, it is generally agreed, are radial dimension of the cell, thickness of the cell wall, amount of lignification, and deposition of dark materials such as tannins, gums, and resins. The first two are rather easily determined under moderate magnification. In contrast, the third can be safely determined only if staining has been done properly or if microchemical tests have been performed. Lignin is concentrated in, but not confined to, the densewood. The dark material mentioned as the fourth feature is visible on unstained sections under a hand lens or naked eye. Of all the features mentioned, this is probably the least diagnostic.

The ordinary conception of a growth layer pictures lightwood followed outward radially by densewood (pl. 1, fig. 1). In the lightwood, the cells are wide radially and possess thin walls which are but slightly lignified. In the densewood, these features are essentially the oppo-

site: the cells are narrow radially and possess thick walls which are more or less heavily lignified. This is the ordinary idea of a growth layer. The features enumerated are not always combined, the three of them together. Can one alone establish the identity of either lightwood or densewood? Or are two necessary? Which two? If the cells are thick-walled and heavily lignified but large in radial dimension, is the wood to be called light or dense? To the unaided eye it would be compression wood. Thick-walled cells, heavily lignified cells, and narrow cells are found isolated, in groups, or in definite patterns anywhere throughout a "normal" growth layer; and the same is true in reverse for the features of lightwood. Since all three do not always occur together, it may be necessary to conclude that the presence of any two of them is sufficient for diagnostic work. A narrow radial dimension, nevertheless, seems to stand out as preeminently characteristic of densewood.

The ordinary idea of a growth layer also has the lightwood giving way gradually to densewood whose distinctive characteristics become more distinctive outward to the abrupt termination of the growth layer. This is not necessarily universal; for instance, in a Chisos Mountain juniper (CMJ 1-1-a), the thickness of the cell walls decreases outward (see pl. 1, fig. 2). Lignification does the same in many instances. In spite of these reversals, the cells gradually become narrower outward and the termination of the growth layer is placed where the narrowest cells lie immediately interior to the very large cells of the next outer growth layer. It seems, therefore, that we have unconsciously but necessarily given more weight to cell size as a diagnostic feature than to the other two.

The whole matter goes deeper than merely the physical or visual features of parts of a growth layer. It concerns, of course, the processes of maturation; more especially, it concerns the vital physiological activity of the cambium. Do wall thickening and lignification increase as the speed of cell division in the cambium decreases? Or do the two continue at the same rate that they held during deposition of the lightwood and only appear to increase because the rate of cell division decreases? Are isolated cells or patches of densewood in lightwood, or vice versa, merely "accidents of maturation" and without significance in cambial activity? A word must be said about radially narrow cells. Densewood cells gradually become narrower outward until the inner tangential walls of the cells come nearly or quite into contact. Is this decreasing cell width indicative of lessening cambial activity, and does a uniform area of cells with minimum radial dimension mean that the cambium over that area ceased all activity

having to do with cell division for a period of time? Extensive observation answers this last question in the affirmative, but at the same time indicates that the cambium is restive, in a manner of speaking, to continue or reinitiate cell division. Witness the many cases of post-seasonal growth.

REACTION OR COMPRESSION WOOD

Compression wood occurs as a common feature in branches of conifers, and especially characterizes Arizona cypress. Although it no doubt exists as a rule along the underside of branches and on the long radius, it is by no means restricted to those regions. It exists as patches, as successive waves, and as crescents anywhere on a section or within a growth layer: on the long, the short, or the quarter radius; in the lightwood or densewood; at the inner or outer margin of a growth layer; in successive growth layers or isolated growth layers; or concentrated on one radius throughout a section or on different radii for each growth layer of a section. Compression wood may extend from the start of a growth layer outward to the outer two or three rows of cells which are densewood normal in all respects. Where it lies along the inner margin of a growth layer and subsides outward into normal lightwood, it may give the appearance of reversed sequence.

The greatest difficulty with compression wood occurs where it lies immediately adjacent to, or bridges, the contact between two growth layers. In most instances, the effect of such wood was eliminated by extra thin sections, by "discounting" its presence, and by the use of high power. In a few cases, compression wood masked critical features to such an extent that the sections could not be used.

The terms "compression wood" or "reaction wood" can perhaps create confusion because they imply an interpretation. A descriptive term would of course avoid such implications. "Brown wood" is descriptive but could be confused with the ordinary densewood of many conifers. In order to avoid confusion, the German word "Rotholz" might be adopted in English in its original spelling, thus making it a technical term.

CONTACTS BETWEEN GROWTH LAYERS

TYPES OF CONTACTS

In 1937, Glock wrote:

The annual ring as it has been used in tree-ring work among the conifers includes the secondary wood formed by the cambium from the time growth starts in the spring until it ceases because of the approach of winter or because of the

exhaustion of the water supply. Springwood is composed of cells which are large, thin-walled, and light-colored, whereas summerwood is composed of cells which are small, thick-walled, and dark-colored. As a rule, springwood merges gradually into the summerwood and the latter terminates abruptly in a sharp outer face. (P. 7.)

Many growth layers, of course, are annual and "normal" in the sense of possessing simplicity as described. Nonetheless, it was recognized in 1937 that the outer face of the densewood of a "false" (intra-annual) ring might so closely approach the sharpness of a true annual as to give a high degree of uncertainty in identification. "There is nothing to do in doubtful cases except to compare the sequence with others, to examine the rings throughout more of the trunk, or to discard the specimen" (Glock, 1937, p. 10). It should be our desire to understand the specimens, not discard them. The reference to an examination of more of the trunk undoubtedly presupposes that (1) the outer face of a growth layer which approaches an annual in sharpness in one area of the trunk will break down to diffuseness elsewhere, thus revealing its identity as a "false" ring, and that (2) *annual* sharpness is a quality distinguishable from any sharpness an intra-annual may have. In reference to point (1) we have found "annuals" which break down to diffuseness and we have noted intra-annuals which, within the limits of our search, maintain their sharpness. Some years of search, in reference to point (2), have failed to reveal any criteria by which sharpness developed at the end of the so-called growing season can be distinguished from that developed by the cessation of growth within a season.

The work upon which this report is based has shown emphatically that the subject of contact surfaces between growth layers is highly complex. As a matter of fact, the subject divides itself into two phases, one having to do with anatomy and description, the other with physiology and cambial activity. The many types of growth layers as marked off by their contacts constitute signposts that act as indicators of that activity to which a description, or classification, of growth layers is a necessary preliminary. An understanding of place, time, and rate of cambial activity depends upon a thorough description and classification of growth layers in all their complications. In this matter of classification, contacts play a highly important role.

Throughout the analyses of the stained microscope sections, four types of contacts were recognized on cross sections, namely, sharp, definite, indefinite, and diffuse. A *sharp* contact is smooth and presents such a decided contrast between the densewood on the inside and the lightwood on the outside (pl. 2, fig. 1: 1941) that no doubt exists

under any magnification as to the abrupt termination of the densewood or to the sudden start of the lightwood. The characteristics of each are possessed to a superlative degree. It is this type of contact which has been emphasized by some as especially characteristic of an annual increment and, in contrast, as not existing among intra-annuals. In the case of the sharp contact, no doubt exists that growth ceased entirely at least for a time, and that the physiologic conditions responsible for the densewood were in marked contrast to those responsible for the following lightwood. Also, the cambium presumably came to rest. A sharp contact, it must be noted, depends as much, if not more, upon the superlative development of the following lightwood as it does upon the accentuation of the preceding densewood. This is less true with stained sections and high powers of magnification.

The term *definite* is applied to a contact if the outer margin is not quite so smooth, not quite so decided as that identified as sharp (pl. 4, fig. 2: 1938). Under high power, it may show slight irregularity. Obviously, however, cambial division ceased for a time. Definite is distinguished from sharp, as a matter of fact, not only for purposes of discussion but also and more particularly for purposes of understanding the nature of the processes responsible for the various types of growth-layer contacts. Such discussion will be held over until the types have been defined. In assembling and synthesizing the results of our microscopic analyses, we have classified all definite contacts with the sharp.

The term *indefinite* refers to undoubted irregularity at the contact or a certain amount of transition from the densewood to the following lightwood (pl. 1, fig. 2; pl. 2, fig. 2: 1939). Under lowest powers of magnification, there is a strong inclination to assume that growth activities merely had declined for a time but had not ceased. High power is necessary to distinguish a contact indefinite because of irregularity or because of transitional features. In the one case growth activities may have ceased entirely; in the other, they probably did not.

The term *diffuse* refers to a contact which lacks any abruptness or contrast between densewood and following lightwood (pl. 2, fig. 2: 1940). Under lowest powers of magnification the transition appears to be gradual and complete. Growth processes responsible for densewood were at first accelerated and later declined, whereas cambial activity probably was continuous but at a decreasing and then increasing rate as the densewood was formed. Under high power the true nature of contacts becomes more clearly defined. Indefinite contacts have been united with the diffuse for purposes of classification in this report.

FEATURES CAUSING DIFFUSE CONTACTS

Indefiniteness or diffuseness is caused by two different combinations of features, the one giving irregularity of contact, the other providing a gradual transition between types of wood laid down. Expressed in terms of cambial activity, the first represents variable but complete cessation of that activity among the cambial initials or variable completion of growth among the last xylem cells set off before cessation, whereas the second actually represents a uniform decline of growth activities followed by gradual acceleration with no interval of complete cessation.

It may be well to describe in some detail the exact anatomical features, seen on stained sections under a microscope, which detract from the simplicity of growth layers as mirrored so commonly on the natural wood. This will, of course, introduce many complexities not considered ordinarily in work having to do with growth layers, complexities that can easily mask the annual identity of a growth layer if sharpness of contact be the only criterion. In practically every instance, the use of high power reveals the presence of those features causing diffuseness. Again note should be made that this investigation has to do primarily with branches of trees, most of which grew under extreme lower forest-border conditions.

Because of the diverse nature of the features causing diffuseness along growth-layer contacts, it is difficult to group them except as (1) those along, (2) those interior to, and (3) those exterior to, the contact.

Resin canals in certain instances are disposed along the surface of contact in such fashion as to yield a certain indefiniteness when viewed under low powers. Even moderate power reveals their identity. Parenchyma cells, dark blue or black under staining, occur isolated, in groups, or in continuous or discontinuous circles. The outer margin of the inner growth layer of 1939 in TTC 33-13-a (pl. 13) appears indefinite because of scattered parenchyma cells within the densewood and along its outer face. Nevertheless, the contact is sharp entirely around the circuit. The long radius of 1941 in TTC 34-20-a² bears waves of compression wood some of whose outer borders are far from diffuse. It is a common thing to find such a fairly definite border, whether on compression or on ordinary wood, succeeded immediately by a row of dark parenchyma cells. In the case of TTC

² Specific examples, rather than general statements, are used to illustrate the features found along contacts and margins although only a portion of the examples appear in photographs.

5-2-a, its growth layer for 1938 bears a row of parenchyma cells along its outer face where it is succeeded outward by an exterior lens. In the sections of XSC 8-1-a, parenchyma cells are associated with the effects of natural frost. The frost and recovery of 1938 are followed immediately by a band of densewood whose outer margin is set with dark parenchyma cells. In the case of the 1938 increment of CMJ 2-1-a, the frost and recovery are in patches separated by cells of densewood and of parenchyma. Such cells give a more or less false diffuseness to otherwise sharp contacts.

A touch of indefiniteness is added to contacts in species normally considered to be lacking in terminal parenchyma cells by the existence of green-stained cells along or just within the contacts. Some of these green cells, which were alive at the time of preparation, are misshapen, some crushed, some collapsed, and some cupped inward. In TTC 34-1, the outer margin of 1938 gives an excellent example of green crushed cells. Furthermore, the outer margin of the densewood is irregular and gives the impression that many of its cells failed to mature when 1938 growth stopped or that extra cells were added here and there after the normal densewood was completed at the end of the season. Studies of densewood immediately interior to the cambium show that both of these alternatives do occur. The phenomena are more decided in 1937 of TTC 34-4-a. Here the outer margin consists of green collapsed cells followed by one to two rows of rather narrow, heavily lignified, thick-walled cells whose outer border is decidedly irregular. It may be that some growth was occurring after the regular growth layer had been finished; in other words, these features appear to indicate certain conditions at the season's end. The above described features, in part probably frost effects on immature (nonlignified) cells, mask or destroy the characteristics normal to densewood. Sharp contacts are replaced by diffuse contacts, and high power serves merely to reveal the cause of the diffuseness.

Features that are interior to the margin and that give diffuse contacts have chiefly to do with the failure of one or more of the characteristics of densewood, such as failure of the cells to remain narrow, failure of normal lignification, or failure of wall thickening. Maturation is held in abeyance or takes place irregularly. In TTC 1-11-d (pl. 6, fig. 2), for instance, the densewood of the outer growth layer of 1943 is feeble and intermittent—intermittent in the sense that radial columns of cells which show no indication of increasing narrowness outward—alternate with radial columns which do show normal increase in narrowness.

Perhaps it is pertinent to emphasize the comparison between the feebleness of the outer densewood of the annual and the strength of the densewood of the intra-annuals (see 1939 of TTC 34-6-a, pl. 14, fig. 2). This emphasis is all the more pertinent because the situation has been encountered repeatedly throughout the work. Failure to lignify normally is well shown in TTP 24-3-b (pl. 19, fig. 1) in which lignification has been fairly normal in the densewood of the inner growth layers but has decreased in the outer growth layers until it is present in such small amounts that the densewoods of the outer growth layers are extremely faint and only visible with great difficulty. In some instances there is not only a failure of lignification but also a failure of wall thickening. The outer cells of the densewood of 1939 and 1941 in Con T 2-0-base b1 (pl. 2, fig. 1) are light colored and thin walled, but narrow in radial direction. The case of Con T 2-7-a has especial interest because the densewood of 1941 is distinct from the earlywood of 1942 over most of the circuit by reason of narrowness of cells only. In different parts of the circuit the cell walls of 1941 densewood and 1942 earlywood may be of equal thickness and equal lignification, or the walls of the earlywood of 1942 may be thicker and more heavily lignified than the densewood cells of 1941, or the cell walls of both may be normal in comparative thicknesses. These comparisons hold true outside of the compression wood. In the case of Con T 1-15-a, the contact between 1941 and 1942 is weak and the densewood of 1941 is atypically developed. The outer three or four rows of cells of this densewood are thinner walled, less lignified, but narrower than those cells immediately to their interior. The same set of features is present in the densewoods of the first and second flushes of 1942 in Con T 2-7-b.

From the above examples, which could be multiplied many times over, it is clear that densewood is not universally a simple constituent of a growth layer, that it has complexities of various types, and that these complexities can detract from the sharpness of contact between the densewood and the following growth layer.

Features that are chiefly exterior to the contact and that detract from marginal definition are varied and intermingled to such an extent that a simple classification becomes difficult. Therefore, no attempt is made to hold a single example to one category. A seemingly irregular rate of cambial activity imparts a ragged outline to a growth-layer margin as seen in cross section. This irregularity is most strikingly shown on the outer margin of the xylem just under the cambium. In fact, a rugose outer face to the xylem is nearly, if not quite, as common as a smooth one. Most certainly the cambium, cell for cell, does not cease activity simultaneously throughout its extent.

In TTL 5-1-a the outer margin of the xylem is partially smooth and sharp and partially irregular, the irregularity being caused by promontories of mature xylem which protrude outward into the phloem region. The cambium loops out around the promontories and perhaps could still have been active because the sections were cut July 25, 1944. However, many examples exist where the sections were cut during the winter (see pl. 7, fig. 1). Sections TTP 24-2-a, for instance, were cut November 29, 1941, and show a highly irregular outer margin of promontories and reentrants on the xylem (pl. 18, fig. 2). The cambial zone has variable width, being smooth on its outer face and filling the reentrants in the xylem with nucleated cells. All cambial cells are large, nucleated, and full of cytoplasm; indeed, it scarcely seems they can be in a resting condition. In the case of TTC 33-10-b (pl. 12, fig. 1), cut January 1, 1943, and many other specimens of Arizona cypress, the irregularity of the outer surface of the growth layer is much finer in detail. Single radial columns of xylem cells protrude outward beyond the general surface. With a unified row of narrow cells as a tangential baseline, contiguous radial columns support from zero to four extra cells thus making the outer surface highly irregular in detail. If the sections had not been cut but had been left to grow another year, what would have been the appearance of the contact on the outside of the 1942 increment? This would depend upon the nature of the lightwood cells laid down upon and between the columns of "postseasonal" cells; the lightwood cells could be normal, giving a diffuse contact, or thick walled and heavily lignified, giving a "curtain effect" or "reverse sequence" (pl. 23, fig. 1). Examples of both are common. If TTC 33-10-b had been cut off during the growing season, we would unhesitatingly say that the cambium was dividing actively. Such irregularities found definitely on the outer surfaces of annual increments constitute simply one type of feature which can mask or destroy the sharpness of an annual increment.

If the xylem responsible for irregularities is formed after the close of the normal growing season, it is called postseasonal growth. It may be represented by an immature cell here and there, by a few widely scattered mature cells, by local patches of cells, or by a layer of cells entire tangentially but incomplete radially as a growth layer. Postseasonal growth, so far as we have observed, may vary from the merest hint up to a nearly complete growth layer. In TTJ 1-1-a and 1-1-b, cut January 11, 1940, scattered immature cells lie just under the cambium. Outward on the branch, in TTJ 1-1-d, the postseasonal growth has been reduced to the merest hint of a cell or two. The sections of TTC 12-14 (pls. 10, fig. 2; 11, fig. 1), cut November 17,

1945, give an excellent example of a series of short lenses of added growth by large-lumened cells around the circuit which represent patches of cells in three dimensions. In TTP 20-23-a (cut November 17, 1944), the densewood of the outer growth layer is followed outward by two to three rows of large, heavily lignified cells making the outer margin indefinite under the cambium and suggesting that another growth layer was in process of formation when growth ceased. This specimen, furthermore, indicates that growth does not have to cease at an accepted point by an accepted group of features such as narrow, thick-walled, heavily lignified cells. The following question might well be asked: If TTP 20-23 had not been cut off in 1944, but say two years later, would it be possible to detect the exact outer margin of 1944 in view of its indefiniteness? In the case of the postseasonal growth on TTC 12-14, what would a further year of growth have done to the margin of 1945?

The above examples illustrate three types of confusion in the delineation and determination of precise outer margins whether they are annual or not. Had the branches been sampled a year or so later, the postseasonal growth would have given either one of two, or both, results: an indefinite outer margin to the previous outer growth layer, or the inclusion of the postseasonal growth in the growth of the following year.

The above considerations must be evaluated in any study necessitating the identification of annual increments without the help of absolute dating methods. The outer contact of an annual increment may be indefinite to diffuse anywhere from zero up to 100 percent around the circuit. If the outer contact is identified as being at the base of the postseasonal growth, then that added growth would be taken as part of the next year's increment and would distort any interpretations based upon measured thicknesses of growth layers.

Marginal definition is also impaired by atypical lightwood. Among the angiosperms (i.e., TTL 5-1-a) a unique situation exists in that one growth layer is composed predominately of vessels and the following growth layer predominately of tracheids (see pls. 3, fig. 1; 36, fig. 2). The growth layers in the sections of TTL 5-1-a were dated with exactness by tip-growth measurements. The vessels of 1943 and the tracheids of 1944, taken together, appear to be one fully developed growth layer, especially because of the indefinite, not to say obscure, boundary between them. Yet the contact is there, the measurements of tip growth demand the presence of two discrete growth layers, and sections 5-1-b, 20 cm. out from 5-1-a, show a more normal development of 1943 and 1944.

A parenthetical statement about compression wood should be made at this point. Ordinarily it would arouse no comment so far as this study is concerned. However, the three growth layers of 1939 in TTC 33-13-b show an interesting similarity between intra-annuals and annuals (see pl. 13). The densewood of the inner growth layer on one radius has a sharp contact under low power whereas under high power the densewood cells show themselves to be merely compression wood. On the middle growth layer the outer contact is sharp except where followed outward by compression wood. High power shows the densewood to be present and sharply bounded completely around the circuit. The outer growth layer has a sharp outer contact except where followed by compression wood. Where this is true of the outer growth layer, the middle growth layer just to the interior is sharp; where the intra-annual is followed by compression wood, the outer contact of outer 1939 is sharp and followed by a normal sequence of lightwood.

Atypical lightwood, whether entirely absent or merely poorly developed, not only impairs marginal definition but also, and what is even more important, reveals information concerning cambial activity. The densewood of one growth layer may merge over an arc of five degrees or less with the densewood to the interior, as in the case XSC 2-1-a where the densewood of the outer growth layer of 1932 "dips inward" to make contact with the densewood of the middle growth layer of 1932 at a sinus (see pls. 14, figs. 1 and 2; 19, fig. 1; 29; 31, fig. 1).³ Or again, the lightwood may be absent over a much greater portion of the circuit, as in TTP 23-1-a (see pls. 17, fig. 1; 25) where the densewood of 1941 lies back against that of 1940. For a short distance the densewoods of both 1940 and 1941 are flush against that of 1939, the microscope showing that only the lightwoods are absent. The sections of TTP 24-14-a (pl. 19, figs. 2 and 3) show a more extreme case in which the densewoods of two growth layers are indistinguishably in contact except for a distance of 10° to 15° where lightwood and an injury are inserted (contrast "added on" lens of pl. 24, fig. 2). Theoretically, the final step should exist wherein lightwood is totally absent around the circuit of a cross section. A method of internal tagging or serial sections would be required to distinguish between two diameter flushes totally lacking in lightwood or to trace them longitudinally into a region where lightwood is inserted. However, longitudinally detached cross sections which show a progressive decrease and final disappearance of lightwood indicate to us that the theoretical condition actually exists.

³ Glock, 1937, pl. 2A, shows an identical instance of merging growth layers.

Poorly developed lightwood detracts from contact sharpness to an extent nearly equal to its absence. Under high power, 1939 in TTP 21-8-a is a complete⁴ growth layer consisting of two to three rows of wide cells and one to four rows of narrow cells. These sizes not only approach each other here and there around the circuit but also approach the sizes of the cells immediately contiguous to them in adjacent growth layers, a transitional feature making it difficult to recognize 1939 at those places except under high power. The next outward growth layer, 1940, is of very irregular thickness and almost wholly thinner than 1939. Under low power this irregularity is seen as a series of short lenses, but under high power it resolves itself into a continuous band of cells around the circuit. The growth layer may narrow to one or two cells in thickness, these being radially narrow and seemingly a part of the densewood of 1939. In places, the inner margin of 1940 is indistinguishable. It is to be noted that the use of high power eliminates the necessity of assuming that the cambium failed to divide throughout an entire season and of concluding that an annual increment is totally absent.

In XSC 1-2-b the outer part of 1935 consists of two entire growth layers. Both outer contacts are sharp except on the short radius where the inner growth layer (under low power) *looks* less sharp than the outer because the lightwood of the outer is reduced to a thickness of one cell which is not as thick everywhere as the lightwood cells at the start of 1936. The point is worth emphasis: the definiteness of a growth layer may depend more upon the characteristics of the succeeding lightwood than it does upon its own characteristics, even though these are definite and sharp. Close study under high power is necessary to reveal true character and definition. Many examples of this have been noted and how many more of the growth layers classed as lenses in our collection actually are entire and complete, only prolonged detailed analysis would reveal.

One more example, TTP 23-4-c (pl. 17, fig. 2), will be sufficient to illustrate the role played by atypical lightwood in marginal definition. The growth layer for 1940 extends four-fifths of the way around the circuit and is made up of lightwood and densewood. Over the rest of the circuit, under low power, the growth layer does not exist—hence 1940 would be interpreted as a lens. High power reveals, however, that over this portion of the circuit 1940 is represented by at least one row of densewood cells. Furthermore, there is variation between

⁴ The term *complete* refers to the radial development of a growth layer and is distinct from the term *entire* which refers to its areal development around the circuit.

adjacent radial columns; for instance, at one place 1940 is made up of one row of wide plus one row of narrow cells, at another place three rows of narrow cells constitute the densewood of 1939 plus all of 1940. The growth layer for 1940 has other weaknesses too; these are below normal lignification and wall thickening. When we move outward and consider 1941, we find its lightwood to be large celled and thin walled, thus making a decided contrast with all of 1940 as well as the densewood of 1939. If these growth layers were not dated by absolute methods, many workers would hesitate to call 1940 an annual increment. Moreover, a lack of close study, not only of this specimen but also of the many others we have had, would merit a conclusion that the cambium had experienced a period of dormancy exceeding a year, whereas close study indicates that the cambium was sluggish, probably very sluggish, but not dormant. It is worthy of note that on tree TTP 23 the cambium in some limbs was highly active, in others like TTP 23-4 it was rather sluggish. This applies with equal emphasis to different areas longitudinally and tangentially in the same branch.

Marginal definition is impaired, finally, by the presence of a transition from densewood outward into lightwood. In nearly all instances, the indefinite contact is due either to subnormal or to abnormal development of the initial lightwood laid down. This type of feature as a cause of diffuseness is more elusive, more confusing, and more conducive to errors of identification, probably, than any of those already discussed. The true features of densewood and lightwood are sufficiently masked to give the student a feeling of uncertainty, and yet they are present with a definiteness to challenge his eyes and his interpretative ability. Back of it all stands the problem of physiological processes as recorded by cambial activity.

Among the angiosperms, growth-layer contacts are at best far from being as clear cut as they are in gymnosperms. Even so, there are varying degrees of diffuseness. The Siberian elm gives a good example. In four different branches of SE 1 the contacts are very indefinite and difficult to locate with precision. They can be located with the use of high power over most of the circuit, but over an arc of more than 90° they are completely indistinguishable. One would be tempted to interpret the growth layers as "false," that is, diffuse intra-annuals, were it not for a late frost injury which occurred in 1938. The contact immediately inward from the frost, annual of necessity, possesses a diffuseness rivaling that of the others. Another point: a hand lens revealed two complete, entire growth layers whereas the microscope showed five. Thus a hand lens can give rise to gross errors.

The Arizona cypress, TTC 30, gives an interesting situation because it grew in a watered flower bed whose soil moisture undoubtedly did not drop below the wilting coefficient. In the densewood of 1939 in TTC 30-1 (cut November 4, 1939), the outer cells narrow somewhat (pl. 11, fig. 3) but are followed outward by wider, thinner-walled, green-stained cells. The transition is so gradual that the complete growth layer is highly diffuse. The outer cells, postseasonal growth assuredly, suggest that growth had occurred right up to the time of cutting and that perhaps a second growth layer was being deposited by reason of a warm autumn and constant irrigation. As a matter of fact, 1939 in TTC 30-2 (cut December 15, 1939) does show two growth layers but also an amount of postseasonal growth equal to that of TTC 30-1. The inner growth layer has a sharp outer contact. The densewood of the outer growth layer grades outward into the postseasonal growth which is like that of TTC 30-1 and thus has a diffuse margin. Growth was incomplete in the sense that the cambium had just divided and that the outermost cells did not mature; the growth layer is incomplete in the sense that densewood was not normally developed and that the contact under the cambium was not sharp. Since the outer margins of 1937 and 1938 are also indefinite, it may well be that the situation in 1939 explains the margins of the former years. These specimens, as well as many others, indicate that differentiation and maturation do not necessarily have to be completed during the season when the cells were set off.

The loblolly pine, Con T 2 (pl. 2, figs. 1 and 2), is of particular interest, first, because it was moved from the Texas Agricultural Experiment Substation east of Lubbock to the Conservatory of Texas Technological College on November 16, 1939, and back outdoors to the grounds of a private residence on April 24, 1940, and second, because the sections came from the trunk. These sections were taken at 20 different levels from near the soil up along the trunk for a span of 240 cm. to the growing tip of the leader. In the lowest sections the outer contact of the growth layer for 1940 was diffuse, and within the span of the next 90 cm. the outer contacts of both 1939 and 1940 varied from diffuse to definite longitudinally as well as around the circuit. The margin of 1940 was wholly sharp around the circuit of sections taken 161 cm. up from the basal sections or 78.3 cm. down from the growing tip of May 18, 1944. This brought the sharp margin within the length of tip growth formed during 1940. Xylem whose appearance would classify it as showing a reverse sequence gives a diffuse margin to 1939 in the sections cut 10 cm. above the basal series where the trunk had been frozen artificially. The first

several rows of cells in the xylem between the outer margin of 1939 and the frost injury of 1940 are larger, thicker walled, and more deeply lignified than the cells of the 1939 densewood. Farther outward, immediately inward from the frost injury, these xylem cells become still larger but are thinner walled and less heavily lignified.

It may well be that growth in the Conservatory location caused the diffuse margin of 1939 because we do know that some xylem was formed while the tree was kept in the Conservatory. The lateness of the season is to be noted, and this is an item in support of the thesis that trees grow whenever conditions are favorable and that their growth is not necessarily confined to one interval per year. Further, it is to be noted that the Conservatory habitat does not directly explain the diffuseness and variability of the 1940 margin.

Another feature having to do with the transition from densewood outward to lightwood is the alternation radially of sharp and diffuse portions of contiguous growth layers. In TTC 5-7 all the contacts for six years have diffuse margins over short arcs of circuit. The outer margin of 1938 in TTC 5-7-b, for instance, is diffuse for more than one-half its circuit; it is diffuse on that part of its circuit where, radially, neighboring contacts are sharp. In TTC 5-8-b and 33-9-a, the increments for 1939 possess three growth layers each. The two intra-annuals in each case can be described as partly sharp, but otherwise complete, entire growth layers. Where one intra-annual is diffuse, its neighbor radially adjacent to it is sharp. If one were restricted to two radii either 90° or 180° apart on these sections, he would have difficulty not only in correlating the sequences but also in making sound interpretations based on growth-layer thicknesses.

The matter of annual contacts showing diffuseness bears so directly upon all growth-layer problems that at least two clear-cut examples must be cited. In TTC 12-10-a, the outer margin of 1939 varies from sharp through indefinite to diffuse. Were it not for methods of absolute dating, one would judge 1939 to be intra-annual if he were committed to the criterion of sharpness as belonging to annual increments alone. The case is more decided even in XSC 11-2-a (pl. 30, fig. 2) where the outer borders of 1937 and 1939 are weak contacts—they are indefinite. Hence, there are fewer sharp growth layers than there are years; the 5-year interval, 1937 to 1941, contained three sharp growth layers. The import of this dearth of sharp growth layers is quite obvious. Our notes for XSC 12-1-a (pl. 32) record eight completely sharp growth layers for 5 years and then continue: "This is the first specimen in more than a dozen that has a surplus of

sharp growth layers rather than an equality or dearth for the number of years involved."

The special features that impart sharpness to a contact are considered, perhaps unconsciously, to reside in the densewood alone. Not infrequently the worker is brought up short by contacts showing apparently a transition from densewood out into lightwood only to realize by close study that the lack of contrast is due solely to atypical lightwood. The preceding densewood is as it should be; the succeeding lightwood fails to give the expected contrast. If the cells do not enlarge, if the walls thicken somewhat, or if lignification is excessive, the sharply distinctive contrast with the densewood fails and, especially under lower powers of magnification, the one growth layer seems to merge into the other. This is illustrated by the outer contact of 1939 in TTP 21-3-b where the margin lacks contrast because in the lightwood of 1940 the cells did not become large. The growth layers of TRSp 1-1-a appear to be indefinite over portions of their circuits because the lightwood fails to contrast with the preceding densewood.

The lack of contrast in lightwood can become somewhat complicated, as in 1939 of TTP 21-2-a. Over three-fourths of the circuit an exterior lens is immersed in what one would call normal densewood under low power. A radial sequence passing outward through the lens is as follows: (1) about seven cells of decreasing widths; (2) from one to three cells exactly like the previous densewood except that their radial widths are somewhat greater; and (3) from one to four narrow cells forming the outer part of the densewood of 1939. The indefiniteness at the inner margin of the lens is not so much a matter of the outer margin of number (1) above—this outer margin is actually quite definite—as it is rather a lack of contrast between the narrow cells of (1) and the only slightly wider cells of number (2) above.

So-called "curtains" give an appearance of diffuseness to the growth-layer margin outside of which they lie (pl. 9, figs. 1 and 2). In XSC 2-3-b, the outer contact of 1938 is highly indefinite; it does not bear those decisive characteristics to be expected in an annual increment. The growth layer for 1939 (see also pl. 19, fig. 1) is in general more heavily lignified than that of 1938 and, in fact, over a great share of its extent it seems to be merely a curtain added on to 1938. Therefore, in XSC 2-3-b we have an example of an annual increment subsiding from the rigid characteristics considered normal for such an increment in contrast with intra-annuals which rise to, and maintain the level of, annual increment characteristics.

Perhaps it is pertinent at this point to mention how transitional margins can vary in their intensity and thus throw doubt on the best

of growth-layer contacts. The sections for TTC 35-7 were cut July 31, 1944. Sections *a* were taken 23.4 cm. inward from tip, sections *b* 17.2 cm., and sections *c* 12.2 cm. In sections *a*, the increment for 1944 contained three sharp, complete, entire growth layers. In sections *b*, the contacts of the three growth layers had deteriorated considerably—they classified as indefinite. Out in sections *c* the three growth layers could be identified chiefly because they had been previously identified in slide *a*. No actual densewood cells were present; larger, thinner-walled cells simply follow radially on thicker-walled cells with little change in cell size. Sharply defined growth layers disappear outward on the branch.

The amount of magnification determines to such a decided extent the interpretation placed upon the results of cambial activity that one wonders whether he dare trust either the unaided eye or very low powers. Perhaps the eye or very low power reveals only the grosser steps in the life record of a tree and misses those more intimate details which actually constitute the life history of a tree or community in success or failure and which we so greatly desire to know. In any event, it happens that the lower the power used, the greater the number of contacts interpreted as sharp. Features of the densewood which detract from sharpness fade under lower powers. The lower the power, the more the eye depends upon contrasts of color and contrasts of light reflection. If, on the contrary, normal densewood is followed by atypical lightwood and the contact appears diffuse to low power, high magnification alone reveals the actual sharpness of contact, especially so on stained sections. In the case of Con T 1-10-a, the wide-field binocular shows three normal growth layers whereas the microscope reveals that one of the growth layers is diffuse over most of its extent.

VARIABLE CONTACTS

Contacts have been described as either sharp, definite, indefinite, or diffuse, which for the sake of simplicity could be grouped as sharp or diffuse, and attempts have been made at definitions. In descriptions of actual specimens, however, it becomes apparent that a single contact as seen on a cross section can and does vary from sharp to diffuse. Variation also occurs in the longitudinal direction. In other words, types of contacts can occur singly or in combination. The general problems arising from variations and combinations are probably best illustrated by specific examples.

The increment for 1940 in TTP 24-14-a (pl. 19, fig. 2) contains three growth layers, the inner one diffuse, complete, and entire, the

middle one partly sharp, complete, and entire, and the outer one sharp, complete, and entire. Over an arc of 15° the outer contact of the middle growth layer becomes very sharp, whereas over the rest of the circuit it is diffuse. And, what is striking, radially outward from that sharp contact is the only place on the sections where the outer growth layer of 1940 has lightwood. The lightwood in itself constitutes a lens. Twelve centimeters outward on the branch, in sections *b*, the inner growth layers are completely diffuse and the outer growth layer has no lightwood. This situation is duplicated 13.5 cm. farther outward in sections *c* save for marked fading of the two inner growth layers. The conditions set forth in TTP 24-14 emphasize the hazards of interpretations based on one radius (note that a certain radius through 1940 on sections *a* would give one diffuse, two sharp growth layers), based on a single section or for that matter on several sections.

The sections of TTC 33-20-a give another pertinent example. As is generally true in TTC 33, 1944 has rather weak contacts in comparison with 1943. The increment for 1944 contains two fairly sharp, complete, entire growth layers plus one fairly sharp, nearly complete, entire growth layer. If we did not know the exact time of cutting (July 31, 1944), if we did not have periodic measurements of tip growth for 1943 and 1944, and if we did not have other specimens also dated exactly for comparative purposes, it would indeed be difficult to determine which growth layers are annual, if any, and which are intra-annual.

Variation of marginal contacts in a longitudinal direction is shown in plates 26, 27, and 28, figure 1, where more of the circuit of a growth layer in the 1940 increment becomes diffuse outward on the branch.

We have found numerous sharp intra-annuals and diffuse annuals. These latter are rare to be sure, we think, but how can one be certain of his interpretations? How is the worker to know whether a boundary, sharp around the circuit on several sections, maintains equal sharpness everywhere? If it should be diffuse over a local area, must it be interpreted as intra-annual? We are confident such a forced interpretation no longer is legitimate. Suppose for a moment, however, that a touch of diffuseness did prove intra-annual character in *all* cases, not just in a majority, then the boundary of every growth layer would have to be examined over its entire area on stem and branch and root. That would be a herculean task calculated to prohibit all interpretative work with growth layers except that of a more restricted botanical nature.

DENSEWOOD STRINGERS

It is not at all uncommon to find the densewood of growth layers, either annual or intra-annual, consisting of as little as a single row, or stringer, of cells. In fact, Arizona cypress is prone to have the densewood of any one growth layer varying from a band many cells thick on one radius to a thin band of one-cell thickness on another, or the opposite radius. The lightwood may likewise vary in thickness from many cells to one cell. Hence, a complete growth layer may consist of one lightwood cell plus one densewood cell, or one densewood cell only, which, in the nature of the case, lies immediately on the outer margin of the densewood of the growth layer next interior. (Many examples of very thin densewoods are to be seen on the plates. See especially pls. 20, 21, 29, 30, and 35, fig. 2.)

Instances are at hand where several such stringers are separated radially from one another by one to three or more cells, one stringer at least being the outer densewood of an annual growth layer. Stringers of the type described pose several problems: recognition, dating, cambial activity, and factors responsible. Only the first two are of concern now. In order to "see" the stringers and recognize them as such, the higher powers of magnification are necessary. Under low powers some of them tend to merge radially into a hazy band whereas others remain nearly, if not quite, invisible. Dating or the differentiation of one annual increment from the other, is a problem of difficulty equal to that of recognition. Some workers unconsciously consider a growth layer to be annual if it has a robust development of lightwood and densewood and they become perhaps unduly suspicious of an atypical growth layer, at times so much so that they refuse to use the sequence bearing it. Thus, a discarded specimen may carry ecologic information of far greater importance than so-called typical specimens.

Many examples could be cited, in addition to the plates already mentioned. The growth layer for 1938 in TTC 36-7-a has an irregular border and, in addition, its densewood varies from a thick to a very thin band. In TRP 2-1-a, 23 cm. back from the tip, all densewoods are mere stringers of narrow cells which are difficult to resolve under any power. Ten cm. outward, in TRP 2-1-b, the densewood zones are thicker and hence the contacts sharper. In XSC 6-3-a, 1939 is described in our notes as a sharp to diffuse, complete, entire growth layer. Much of its densewood is an irregular stringer, a single cell thick, which lies one to two cells out from the 1938 densewood. In fact, the multiple densewood of 1938 plus the indefiniteness of 1939

gives the sequence 1938 to 1940 an uncertainty which would make dating impossible were it not for the 1938 frost injury, a knowledge of the cutting date, and crossdating with previous specimens. The annual increments do not have sharp borders and are otherwise atypical but do not have to be discarded.

COMPLETENESS

A growth layer may be considered complete if densewood has been formed. Ideally, the only complete growth layer should be the sharply bounded one, the one which supposedly records complete cessation of cambial activity. However, the presence of sharply bounded densewood cannot be the only criterion of completeness because then the difficulties of description and understandable nomenclature would be almost hopelessly great. It is the margins which are not sharp that give the complexities inherent in the problem of completeness. (For incomplete growth layers, see especially pls. 31, fig. 2, and 35, fig. 1.)

SUMMARY AND CONCLUSION ON CONTACTS

The unaided eye and low magnifications encounter a minimum of trouble with growth-layer contacts. Perhaps this is a boon for certain types of work. Even if work based on low magnification were ultimately proved fairly accurate, it would still touch only the high spots, not necessarily the critical, in the life history of a tree.

High powers reveal many features not otherwise visible, as well as the great amount of variation along growth-layer contacts—the one carrying a more complete history, the other a more accurate history of cambial activity than that obtainable otherwise. Complexity, not simplicity, characterizes many growth-layer margins. Hence, it follows that cambial activity is at least equally complex and, indeed, more so if the significance to the classification of growth layers is used as a criterion.

Contacts may be sharp, definite, indefinite, or diffuse, and may possess graduations between any two. On any one cross section the outer margin may be entirely sharp, or entirely diffuse, or the one circuit may contain all types of contacts. Similar unity or variation extends in the longitudinal direction. As a matter of fact nearly any growth layer, no matter how sharp appearing under low power, yields its sharpness under high power to a greater or lesser extent somewhere on the circuit by reason of one or more of the features discussed under causes of diffuseness. In contrast there are examples,

not too plentiful, where high power alone reveals the true sharpness of a contact.

Our work amply shows that weakness of contact does not avoid annual boundaries. Assuredly it would lend simplicity to the matter if sharpness were restricted to the outer borders of annual increments and diffuseness to intra-annuals. Extensive work may ultimately prove that an intra-annual will break down from rigid sharpness somewhere in its total area. One could perhaps be excused for the hope that this will be proved true. Nevertheless, any such startling simplicity seems at present to be ruled out—a percentage of annual contacts shows weaknesses, and a percentage of intra-annuals shows strength. The conclusion is verified by absolute dating.

CLASSES AND TYPES OF GROWTH LAYERS

Classification is here considered as a display of the various anatomical forms presented to us by growth layers in the xylem. Such a more or less orderly arrangement is considered merely a first step, an adjunct, in the complex problem of cambial activity. Only when we learn something of the intricate nature of cambial activity, its time of occurrence, rate and place of cell division, and interrelationships, can we hope to inquire into the environmental factors which directly and indirectly, separately and combined, influence that activity.

Growth layers are classified as either entire or partial.

ENTIRE GROWTH LAYERS

Definition.—The term *entire* as applied to a growth layer signifies that the growth layer is continuous around the circuit of the tree sections under study, that nowhere on the circuit does the lightwood of the growth layer succeeding it make contact with the densewood of the growth layer preceding it. The term is, of course, equally applicable to the presence of the growth layer over the whole body of a tree. However, in this report it is used in connection with the branch or portion thereof under study at the time. Examples are shown in plates 1, figure 1; 8; 10, figure 1; and 14, figure 2.

Types of entire growth layers.—The *annual*, in which one entire growth layer constitutes the annual increment, is probably the most common type of growth layer in certain geographic regions. In plate 1, figure 1, the growth layer for 1938 is very close to being a single, entire, annual growth layer (see also pl. 2, fig. 3).

The *intra-annual* type is less common than the annual except in some trees of certain regions and in some years, where the intra-

annuals actually outnumber the annuals. The increments for 1938, 1939, and 1940 on plate 32 contain examples of this type. As was pointed out heretofore, the outer margin of any growth layer can vary around the circuit from sharp through all gradations to highly diffuse. Entire intra-annuals exhibit all these gradations as do true annuals, though the latter do so far less frequently. Workers have applied the terms "false" or "double rings" (Antevs, 1925, pp. 123-124; Douglass, 1928, pp. 31-32; Glock, 1937, p. 10; Hawley, 1941, pp. 31-33) to growth layers obviously intra-annual because of their diffuse margins. A diffuse "double" is easily detected but this is far from true with sharp doubles. In fact, the whole of our work emphasizes the impossibility of distinguishing a sharp intra-annual from an equally sharp annual. We can go a step farther. What we have called a *thin outer* growth layer (pl. 30, fig. 2), terminating the annual increment, commonly possesses densewood so weak in its total development as to appear indefinite, whereas the inner growth layer—the actual intra-annual—possesses a strongly developed densewood whose outer margin is sharp. The status and significance of this outer thin growth layer will be discussed more at length in the chapter on multiplicity.

Structurally, an intra-annual consists of an entire circle of densewood immersed in the lightwood zone of an annual increment. It may comprise, on the one hand, a densewood zone equal to or more accentuated than that of the annual increment itself; on the other hand, it may be merely a touch of added lignification, slight wall thickening, slight narrowing of the lumens, or a combination of these phenomena. It may be part of an independent, sharply margined growth layer in every sense of the word; it may be strongly developed on one radius and more or less weakly developed on the opposite; in either lateral or longitudinal dimension it may run the gamut from strength and sharpness through increasing weakness and diffuseness to total replacement by the normal lightwood of the annual increment.

In the study of growth layers a knowledge of the complexities of classification is an absolute necessity, even for a preliminary understanding of cambial activity. Physiologically, all the types of intra-annual growth layers furnish us a picture of the intricate variations in cambial activity and in the processes of cell maturation.

Entire growth layers may be separated into two types on their relative completeness. An *incomplete* growth layer does not have a finished sequence of lightwood and densewood radially. In like manner, then, a *complete* growth layer does have a finished sequence. These two types may perhaps be translated into physiological functions by

recognizing that cambial activity has not slowed down perceptibly in the one type and has ceased completely for an interval of time in the other.

In general practice, the two types, incomplete and complete, are applied specifically to the outermost growth layer of the cross section. Sections cut at different times in the growing season show varying degrees of completeness in relation to the formation of lightwood and densewood (pls. 4, fig. 1; 24; 25; 29; 30, fig. 1; 31; 35, fig. 1). This is to be expected. Sections cut after the end of the so-called growing season and exhibiting a certain degree of incompleteness on the margin of the outermost growth layer bear directly on the problems of postseasonal growth, of growth layers with indefinite margins, and of growth during what is considered the normal rest period (pls. 10, fig. 2; 11, fig. 3; 12, fig. 1; 16, fig. 2; 17, fig. 1; 19, fig. 3). These problems of the outermost growth layer must be recognized in order to understand the reasons for the many types of margins on growth layers when they come to be overlaid by later xylem. Although completeness appears of paramount importance to the most recently formed growth layers, we nevertheless kept accurate record of all growth layers.

If we turn from the anatomical aspects to the physiological, the subject of completeness becomes highly complex. The cambium neither becomes active as a unit nor rests as a unit, and this holds true no matter what the time of year. Initiation and cessation of activity are not radial exclusively; they may be tangential, producing lines of demarcation at an angle between the radial and tangential directions. In this connection, note is made of the densewood of a thick lens. On one radius the cambium may have been at rest, while on another, several radial columns of cells away, it seems to have been dividing actively. A so-called half-lens is the result (pls. 6, fig. 2; 22, fig. 1; text fig. 9).

Completeness, in summary, is a radial affair whereas entirety is tangential. The two together aid in giving at least a partial picture of cambial activity in time and in space—in time, at any time during the growing season or during the rest period, and in space, anywhere in the plant body. The two together give us growth layers of great variety, a variety which the present attempt at classification hopes in part to clarify.

PARTIAL GROWTH LAYERS

Definition.—The term *partial* as applied to a growth layer signifies that the growth layer is not continuous around the circuit, that some-

where on that circuit the lightwood of the growth layer succeeding the partial one makes contact with the densewood of the growth layer preceding it. In a general sense, the term is applicable to the growth layer anywhere over the tree body; in a restricted sense, it is applied to a cross section but with full knowledge that the characteristics shown on the cross section may, and commonly do, persist in a longitudinal direction.

Simplicity in connection with partial growth layers from a lower forest-border locality is a desideratum not apt to be granted. From an ideal standpoint, a partial growth layer possesses lightwood and densewood, both of which fall short of completing the circuit. There are, however, growth layers whose lightwood is partial and whose densewood is entire. How should these be classified? Are there partial growth layers which have no lightwood at all? If so, and if the densewood cells of the partial growth layer lie flush against the densewood of the growth layer next interior, then identification would be nearly, or quite, impossible. Could a partial growth layer composed of densewood only be located elsewhere, say within the body of a complete, entire growth layer? The matter depends upon time, rate, and site of cambial activity; upon the interrelationships of one part of the cambium to other portions of the cambial sheath; and upon the rhythm of the growth processes.

Partial growth layers may be either closed or open. In a *closed partial*, the lightwood covers a shorter arc (or smaller area) than the densewood so that the latter overlaps and extends tangentially (and longitudinally) beyond the lightwood. In an *open partial*, on the contrary, the lightwood extends beyond the termination of the densewood.

Types of partial growth layers.—Partial growth layers have been subdivided into lenses, half-lenses, temporary lenses, arcs, divided densewood, divided lightwood, interrupted densewood, interrupted lightwood, curtains, and postseasonal growth.

Lenses are closed partial growth layers; the lightwood covers less area on the tree body (shorter tangentially on a cross section) than the densewood which always makes contact with the densewood of the growth layer next inside. Stated somewhat differently, a lens contains the xylem produced by localized cambial activity. The ideal lens is a patch of xylem of rather complicated geometrical design which has, in general, the complex features of a truncated, partially developed cylinder and cone. In cross section a lens appears concavo-convex, whereas in longitudinal section it is nearly plano-convex. Lenses cover anywhere from zero to 100 percent of the plant body.

At 100 percent, of course, a lens becomes a complete, entire sheath. On cross sections, lenses vary in length from 0° (pl. 8) up to 360° (pl. 14, fig. 2) around the circuit. Many lenses occur on the long radii of branches and constitute the reason for the longer radius, but they are not necessarily confined to that radius. If the long radius is due to local thickening of the entire growth layers, lenses may be the means of reestablishing concentricity of the woody cylinder.

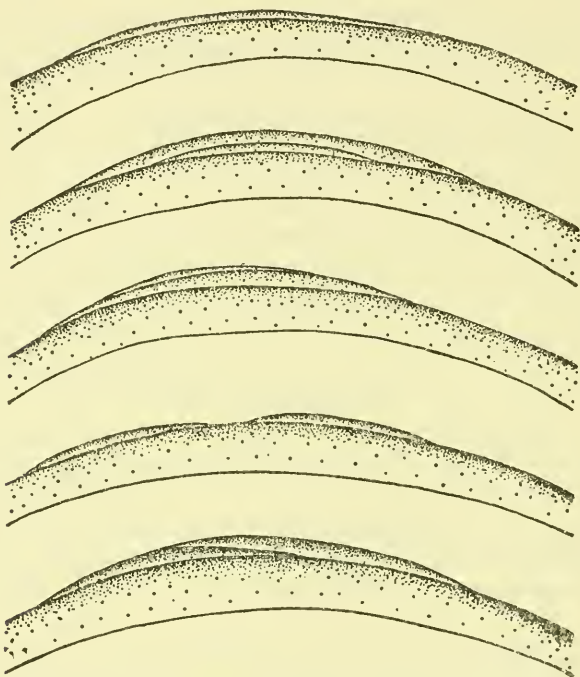


FIG. 1.—Various types of lenses. In order from top to bottom: Simple lens, compound lens with outer one the longer, compound lens with inner one the longer, concurrent lens, overlapping lens.

The term "lens" as here used refers to the same feature previously designated as locally absent (Douglass, 1935, p. 68) or locally present (Glock, 1937, pp. 8-9). These last two have been abandoned because they are not sufficiently descriptive, not sufficiently flexible, and cannot be applied to transitional forms.

True lenses occur in several varieties. The *simple lens* (text figs. 1, 2; pl. 8) is single and corresponds in cross section to the ideal concavo-convex form previously described. It may be either interior or exterior in its relationships with the complete, entire growth layer to which it seems most closely related. If we think of the cambium as

having major intervals of activity, whether one or several annually, then local activity immediately preceding the major interval produces an interior lens, and local activity immediately succeeding the major interval produces an exterior lens. Examples of interior lenses are shown in text figures 3 and 4 and in plate 20; examples of exterior lenses are shown in figure 4 and in plates 8 and 13.

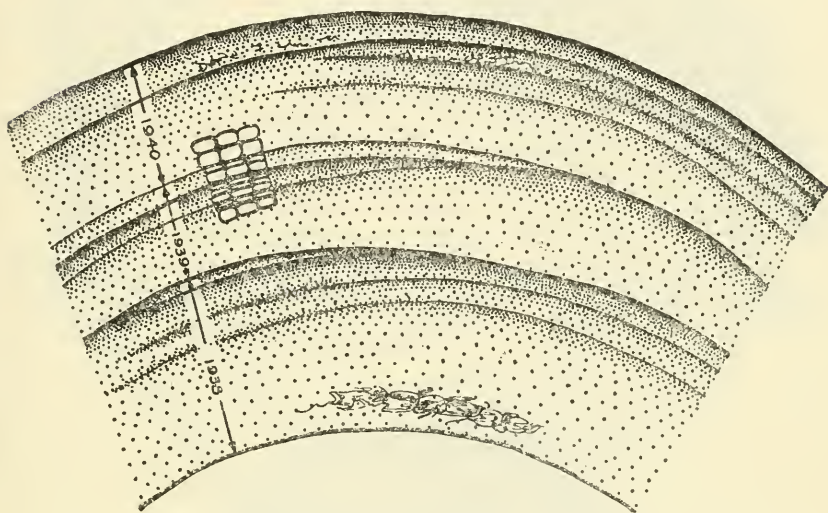


FIG. 2.—XSC 8-4-a. Multiplicity and partial gls* by symbol and cell structure. 1938: Effects of natural frost; 2 s arcs becoming diffuse and disappearing into lightwood; sce; sL; 1939: sce; 2 sL, outer dw of inner sL is heavy, outer sL made up of 2 rows of cells, 1 of lw and 1 of dw; 1940: 1 s arc becoming diffuse and disappearing; d $\frac{1}{2}$ L disappearing; 2 sce.

* Abbreviations explained on p. 101.

A *compound lens* consists of two or more lenses in contact with each other and in sequence radially (text figs. 1, 2, 4; pls. 8, 13); they represent two or more successive intervals of cambial activity. In some cases the inner lens possesses the greater area, in others the outer, dependent upon a decrease or an increase in area of cambial activity. The rate of cambial activity may vary at one locality on the circumference, thus giving a series of lenses which represent an alternation of rapid cell division and little or none, during the general growing season. This is well illustrated by a highly eccentric growth layer whose bulge consists of a radial series of lenses (pls. 8; 13; 22, fig. 1; 29).

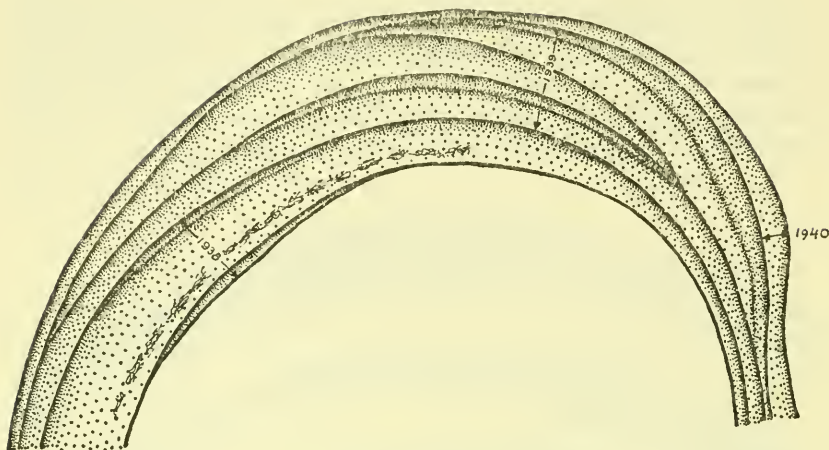


FIG. 3.—XSC 1-4-a. Increments for 1938, 1939, part of 1940. Complex nature of cambial activity, shifting localized activity; interior lens; double overlapping lenses.

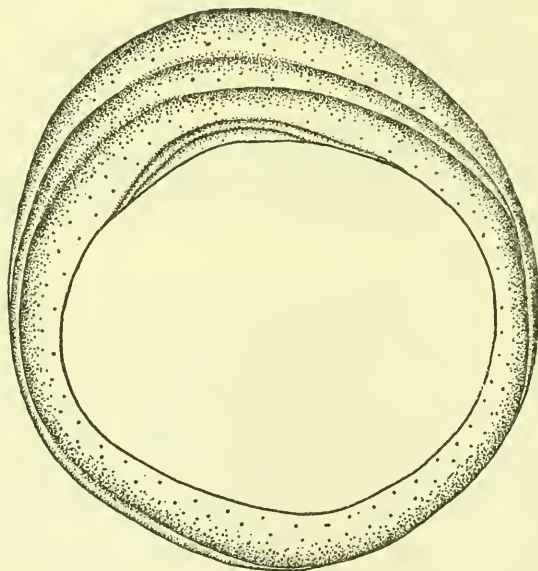


FIG. 4.—XSC 3-1-a. The increment for 1939. Multiplicity and partial gls. Sequence as follows: compound dL; msce, the chief gl; msL; sL overlapping the msL.

A *concurrent lens* consists of a system of two or more lenses around the circuit, not in contact radially (text figs. 1, 5, 6, 7; pl. 36, fig. 2). Commonly they lie between two complete, entire growth layers, and represent localized cambial activity completely or partially simul-

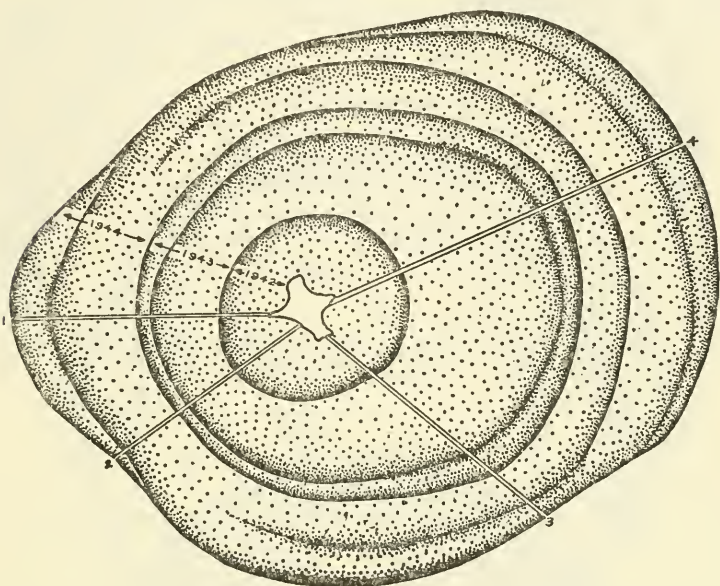


FIG. 5.—TTC 33-6-a. Increments for 1942-1944. Variable number of gls on different radii. 1942: sce; 1943: msce; sce; 1944: long s arc (probable variation in cambial activity producing no visible effect between points of arc); msce; concurrent lenses. Sequence of sharp or diffuse contacts along numbered radii:

1	2	3	4
s	s	s	s
s	s	d	d
s	s	s	s
		d	s
d	s	s	d
s	s		s

Other radii give different sequences.

taneous but always occurring between the major episodes of cambial activity. Although composed of two or more discrete lenses on a particular cross section, the combination is considered a unit for purposes of description in the chapter on multiplicity.

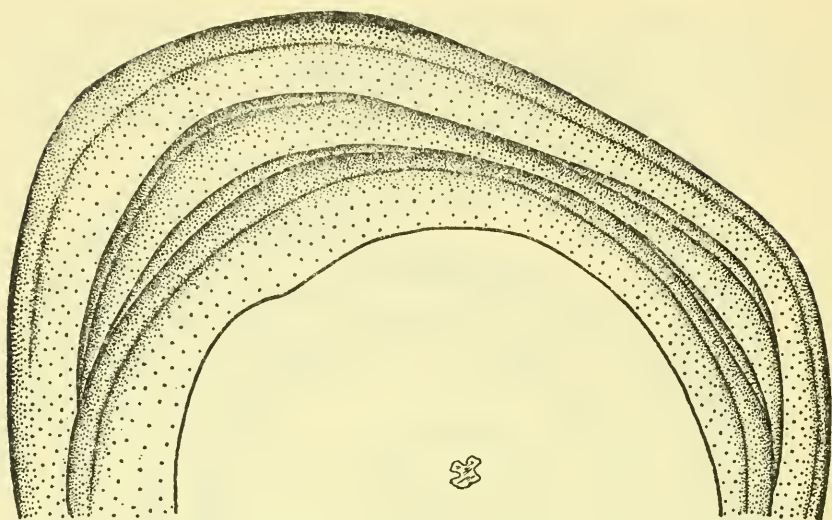


FIG. 6.—XSC 1-3-c. Increment for 1937. Complex lensing; two series of concurrent lenses. Different sequences on different radii.

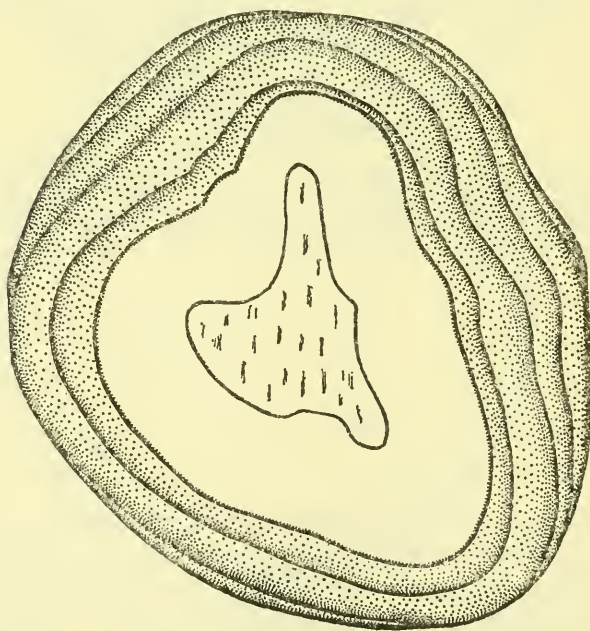


FIG. 7.—YCt 2-5-a. Increment for 1940 (probably). Multiplicity; rather complex situation of compound and concurrent lenses.

An *overlapping lens*⁵ occupies in some respects an intermediate position between the two foregoing varieties. If the lens is compound but the two units are not centered on the same radius, an overlapping results as shown in text figures 1, 4, and 8, and plate 22, figure 1. Such lenses are not too common in cross section. However, if the whole plant body is considered, it may be doubtful that a true compound lens ever exists; somewhere over its area it will no doubt be overlapping.

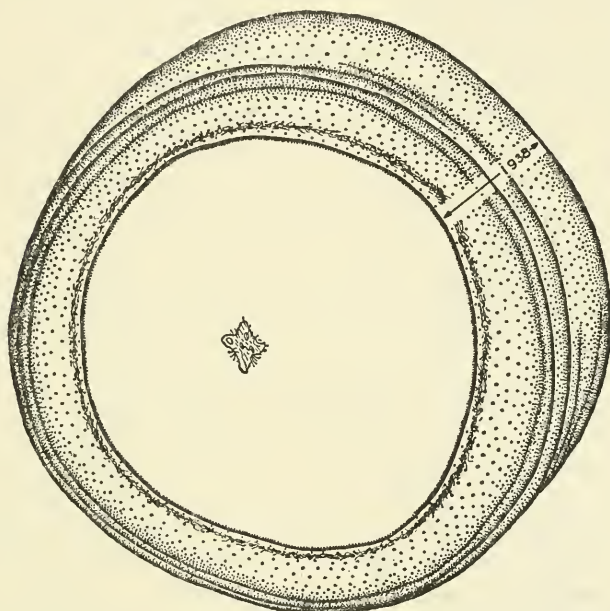


FIG. 8.—XSC 1-2-a. Increment for 1938. Outside the frost circle there appears: psce; long sL (nearly sce); thick sL, compound with former sL, and containing overlapping $\frac{1}{2}$ L's and compound $\frac{1}{2}$ L's.

The last variety of lens to be discussed here is called, for want of a better name, a *low-power lens*. Under low power, and especially under a wide-field binocular or a hand lens, only a single lens or a concurrent lens is visible. Under high power, on the contrary, it is seen that only the lightwood terminates at the cusps, the densewood continuing around the circuit as a layer one to several cells thick flush against the densewood of the growth layer next interior to, and indistinguishable from, it (pl. 7, fig. 2). In TTP 21-6-a the increments for 1939 and

⁵ At first this was called transgressive because a band of densewood appeared to transgress the lightwood separating two major bands of densewood.

1940 are invisible in their entirety except under high power (pl. 19, fig. 1, is suggestive). The increment for 1939 on the cross sections consists at places of one wide and up to two narrow cells radially; elsewhere it consists merely of one row of densewood cells difficult to distinguish from the previous densewood zone except by continuous tracing around the circuit from the place where the lightwood ends. Under low power the increment for 1940 appears to be a long lens, whereas, actually, the lightwood only is lenticular, the densewood being entire. Some radial rows in the portions composed of densewood exclusively fail to narrow down, a feature that adds a touch of indefiniteness to the combined bands of densewood.

In TTP 24-3-a, 1939 is easily visible under low power as a concurrent lens of two units, whereas under high power it is seen that only lightwood is lenticular and that the densewood is continuous around the entire circuit as a layer two cells thick. No visible boundary separates 1938 from 1939 where their densewoods are in contact. Because of the nature of 1939, the outer margin of 1938 appears to be indefinite except under high power. The outer margin of 1939 likewise varies from sharp to indefinite, but on the whole it is sharper than that of 1938. The increment for 1939 is, in general, a very thin growth layer; in detail it is, of course, variable in thickness.

Marked differences in interpretation appear when a growth layer like 1938 above is analyzed under high power. First, reference is made to cambial activity. Low-power analysis would indicate cambial activity completely localized throughout the span of an entire growing season. If the lenticularity is due to a lack of water, as some have supposed, then available soil moisture must indeed have been of nearly negligible amount. Furthermore, such an analysis requires portions of the cambium to forego cell division from the end of one growing season until at least the beginning of the growing season second removed from the first. There may be a question in some minds that portions of normal cambium can remain in respiratory and metabolic balance over such long intervals in the presence of photosynthesis and without a break in the hydrostatic system. Analysis under high power reveals an increment entire around the circuit and a cambium active throughout the same extent. It was active, to be sure, yet so sluggish that it deposited very little lightwood and this was lenticular in distribution. Can the sluggishness be ascribed to any one environmental factor? Other branches of the same tree do not all agree in this lack of high activity.

The increment for 1939 in TTP 24-3-b (pl. 19, fig. 1), 6.5 cm. outward from 24-3-a, is somewhat more definite and hence more easily

distinguished than in sections *a*. However, in TTP 24-3-c, 5.5 cm. outward from 24-3-b, our analyses of 1939 say: "An excellent example of the *annual* type of divided densewood.⁶ The densewood of 1939 lies immediately against the densewood of 1938 over most of the circuit; where it does not, the insertion of incipient (only partially developed) lightwood cells makes 1939 visible under low power for half this latter extent, the other half of this small part of the circuit being visible under high power only." The increment for 1939 possesses characteristics which make its identification quite impossible except on stained sections under high power. All this would be in the nature of assumption were it not for methods of absolute dating and a coordinated series of slides. For instance, the visible "lenses" of 1939 bear injury by late spring frosts near their interiors. In TTP 24-3-d, 10 cm. outward from 24-3-c, 1939 has been reduced to such an extent that only faint hints of its presence remain: "A slight touch of frost in some sections and the merest hint of divided densewood."

Second, reference is made to the transition toward which growth layers of such reduced radial dimension appear to be pointing. It seems obvious that complete transition exists from an entire growth layer normal radially, to an entire growth layer with lenticular lightwood, and to an entire growth layer whose lightwood has been so much farther reduced that the only visual evidence of the growth layer is what we call divided densewood. Perhaps the last vestige of lightwood disappears, the combined densewoods appear as a unified band, and the record of a distinct interval of cambial activity becomes invisible. In the case of TTP 24-3-a, our notes of November 1946 state: "The intimate contacts of the densewoods of 1939 and 1938, and of the interior concurrent lenses of 1941 with the densewood of 1940, resemble closely what we have been calling divided densewood in the descriptions of previous sections. Heretofore, divided densewood has been thought to be of little consequence. Now we find, however, that divided densewood and even undivided densewood may represent two distinct intervals of growth or, further, two separate seasons. Divided densewood where seen prior to this time is certainly one form of multiplicity." Note especially plates 31, figure 1; 10, figure 1; 5, figure 2; 23, figure 2; 25; 13; and 19, figure 2, for gradations in divided densewood.

Half-lenses may be thought of structurally as open lenses; that is, at one edge on a cross section the growth layer closes in a cusp with lightwood and densewood wedging out against the densewood either of the preceding or succeeding growth layer, whereas at the other edge

⁶ Divided densewood is considered in some detail later in this section.

the densewood feathers out into, and the lightwood merges into, the lightwood of the general growth layer. This appearance on cross section applies equally well to that in area over the whole tree; that is, part of the densewood termination lifts away from contact with other densewood and "floats" free in lightwood.

Half-lenses are simple or compound depending upon the presence of one, or more than one, in a single system at one locality. Text figure 9 shows three simple and one compound half-lenses. On a dif-

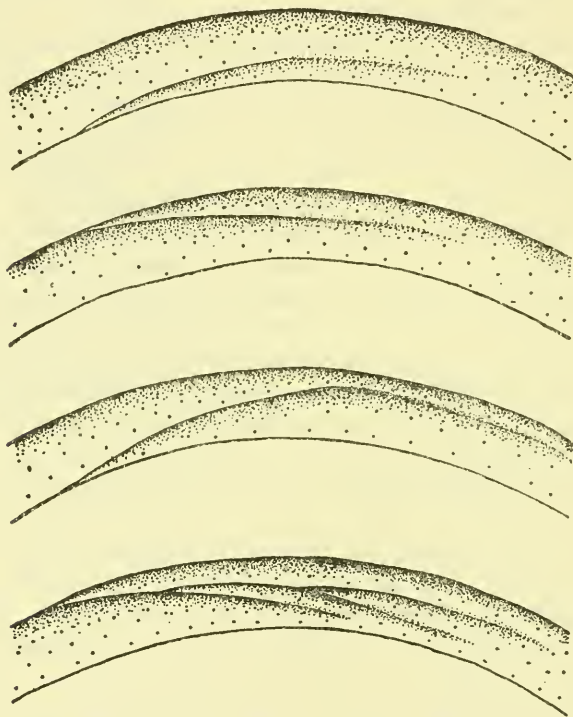


FIG. 9.—Various types of half-lenses. In order from top down: interior half-lens, exterior half-lens, thick interior half-lens, compound exterior half-lens.

ferent basis, half-lenses are either interior or exterior. In the interior variety, the cusp terminates against the densewood of the preceding growth layer (text fig. 9); in the exterior, the cusp terminates against the densewood of the succeeding growth layer. Text figure 10 shows not only an exterior half-lens but also an exterior lens.

Two phases of the subject merit somewhat more extended discussion. They are the identity of the half-lens and the nature of cambial activity. In the structural picture the half-lens on cross section

appears to be simply a lens whose one cusp has come free from the neighboring densewood. Structural character has been altered at once. The half-lens becomes a feature of the main growth layer (text fig. 10) whereas the lens is a patch of xylem added onto the main growth layer—a great difference. If the cusp drops inward, then the half-lens is an exterior one; it is a feature of the inner main growth layer and is the result of an irregularity in the main episode of cambial activity and growth processes producing the inner main growth layer. If the cusp rises outward, then the half-lens is an interior one; it is a feature of the outer main growth layer and is the result of an ir-

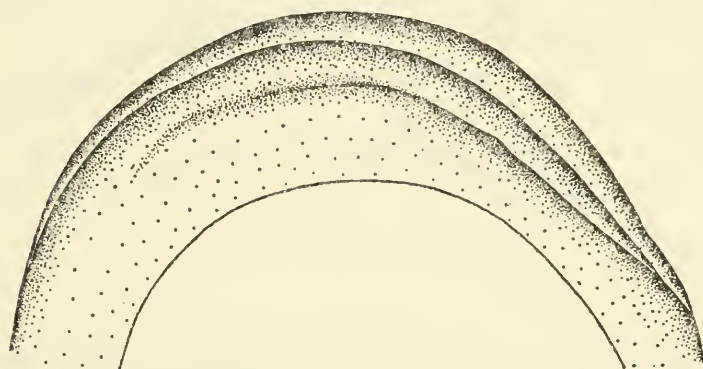


FIG. 10.—XSC 1-2-a. Part of increment for 1939. Lensing: $\frac{1}{2}$ L; sce; sL.

regularity in the main episode of cambial activity producing the outer main growth layer. This linking of the half-lens to a lens leads to some confusion as to the exact identity of the half-lens.

The problem can perhaps be clarified by reference to text figure 11. Initial attempts at classification, it now appears, considered merely the band of densewood, *b* (text fig. 11). But densewood alone is only part of a radially normal growth layer. If densewood, *b*, at some place longitudinally moves out to join *d* at both tangential extremities, then *c* would constitute a proper lens. Is *c-d* in the figure the half-lens? Or is it *a-b*? The lightwood *c* is visibly continuous with lightwood E and yet the cambial activity which resulted in the segment *a-b-c-d* has had a different history than that at E or F. From the standpoint of cambial activity solely, *a-b* is the half-lens, set off as a feature by localized cessation of that activity. The history of the cambium has not been uniform as regards rate and place of activity or change of rate and change of place. If *a-b* be taken as the half-lens, cambial activity slows or ceases locally for a half-lens and, in contrast, remains active

or resumes activity locally for a lens. It must not be forgotten that somewhere on the area of a half-lens the free edge of the densewood no doubt "migrates" so as to join a contiguous band of densewood.

The sketches in text figure 12 suggest a different mode of origin for half-lenses. Although five stages are given, all manner of transitions have been observed. Our cross sections show many examples of stages 2 and 3 (see pls. 3, fig. 1; 6, fig. 2; 8; 22, fig. 1; 24, fig. 1; 29, and others).

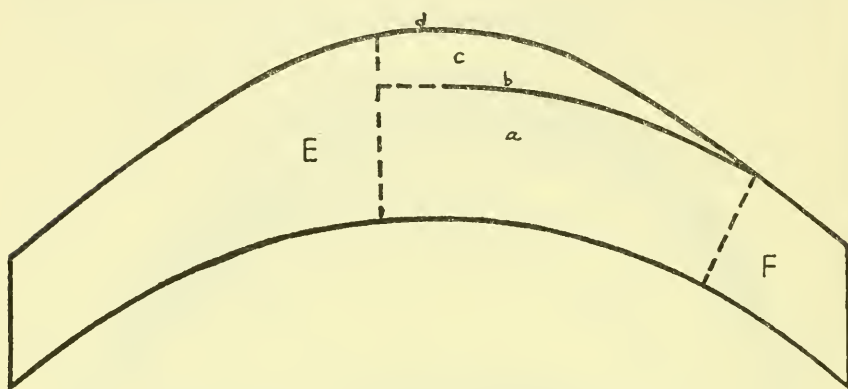


FIG. 11.—The problem of the half-lens diagrammatically expressed. Densewood, *b*, taken by itself is not the half-lens. Sequence *a-b-c-d* should be interpreted in terms of cambial activity and maturation processes.

The identity of the half-lens is not easy to visualize in three dimensions. Structurally, classification need only be descriptive; but physiologically, classification should be as nearly genetic as possible, serving as a guide to the course of cambial activity and variation of growth processes.

The matter of cambial activity becomes complex indeed. Text figure 13 shows the complex part of the annual increment for 1939. Over more than half the circuit 1939 is a growth layer of fairly uniform width. A circle of dark parenchyma cells extends entirely around the circuit at a uniform distance from the start of the growth layer, thus indicating that the rate of cambial activity was uniform throughout most of the growth. Later, a portion of the cambium became intermittently active, the activity punctuated by intervals of slow and of no growth. As a result, 1939 bulges outward in a series of lenses and half-lenses. The temptation is strong to call B and E (text fig. 14) the half-lenses rather than A and D. To say that B and E are the half-lenses is nearly tantamount to saying that a growth

layer can begin with densewood and end with lightwood. The densewood of A_1 is equivalent tangentially to lightwood in the region A_2 . Conditions at one place gave densewood, at another lightwood. Was the pause in cambial activity at the densewood of A_1 brief or was the formation of lightwood at A_2 a very slow process?

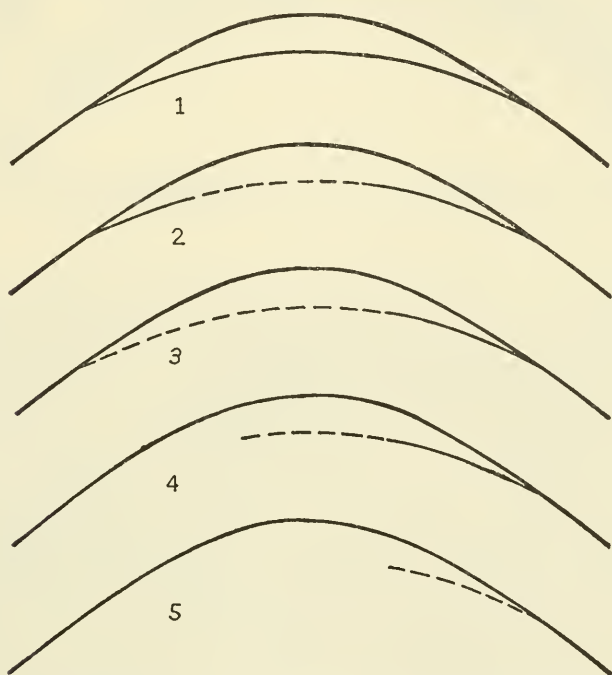


FIG. 12.—Suggested transitions from lens to half-lens, and disappearance of the latter. A study in variation of cambial activity and maturation processes.

The whole system of lenses in 1939 is a mixture of compound, overlapping, and, in a certain sense, transgressive lenses and half-lenses. Lenses C and D (text fig. 14) are not quite centered on the same axis. They are compound in a certain sense, notwithstanding the fact that D overlaps C slightly. The densewood bands at the inner and outer margin of lens C unite to the left with an outer band of densewood at Y and Y_1 ; to the right they unite at X and X_1 with an inner band of densewood, that of the half-lens, A_1 . If we consider the bands of densewood alone, the bands Y-X and Y_1-X_1 transgress outward across the lightwood, B-C-D, from the densewood of the half-lens to the densewood at D which constitutes the outermost part of the annual increment. Sections XSC 1-1-a, 13 cm. inward, show the same lens system save that margins are somewhat less definite.

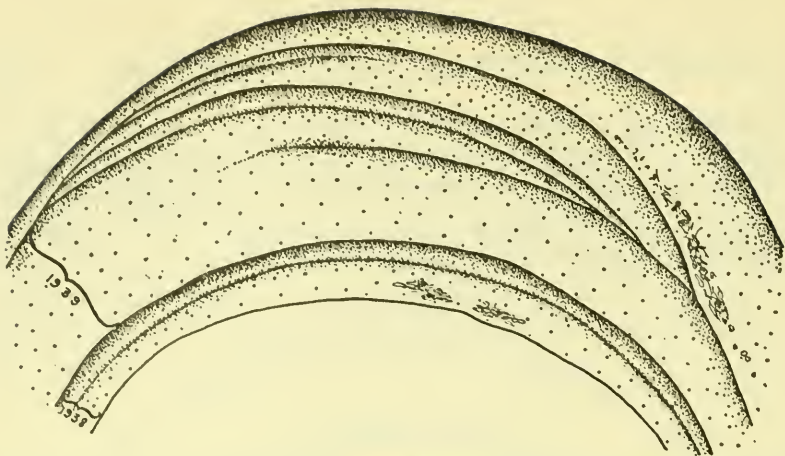


FIG. 13.—XSC 1-1-b. Increments for 1938-1940. Lensing. Interpretation shown in figure 14. 1938: Effects of natural frost; dce; sce; 1939: $\frac{1}{2}$ L; msce; sL; $\frac{1}{2}$ L; sL overlapping previous sL; 1940: effects of natural frost; sce.

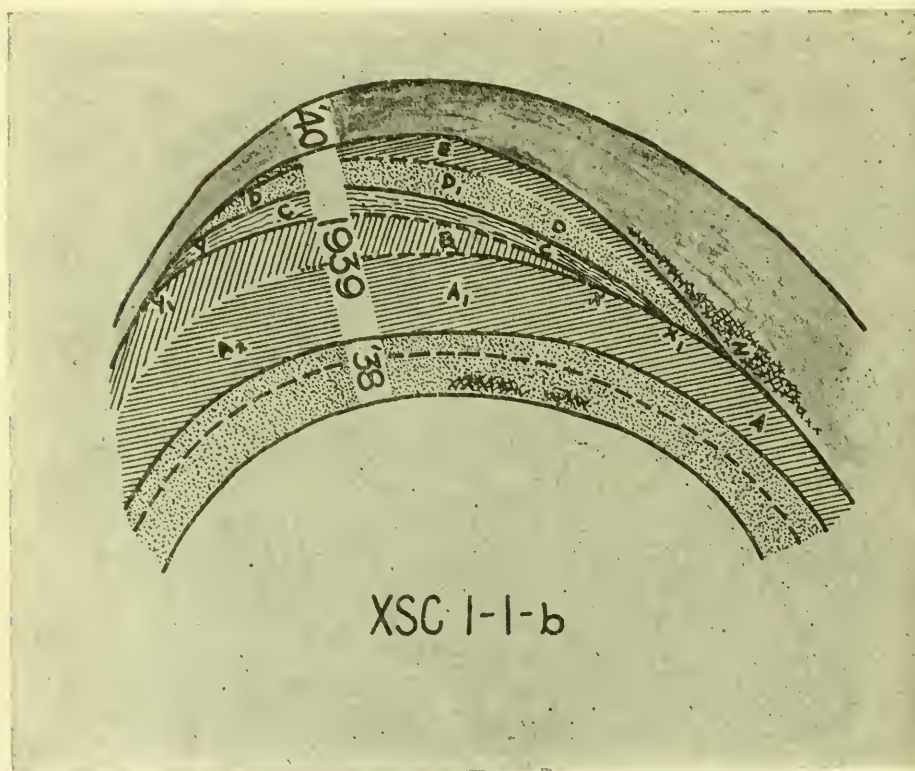


FIG. 14.—An interpretation of figure 13. Localized and periodic activity of growth processes. Contacts sharp, diffuse, or invisible. Dw at first sharp, then diffuse, then nonexistent as an "invisible" contact (long blank space); hence, half-lenses become actual lenses. Letters A to E give successive episodes of cambial activity. Dw of A becomes diffuse. A₁ and disappears to the left where the blank space represents an invisible contact, i.e., no dw developed. C overlaps B, D overlaps C, and E and D are a compound lens. Dw of D fades at D₁ and an invisible contact is pictured as continuing the dw (half-lens) in order to produce a relatively simple lens. Such interpretation simplifies the picture of cambial activity, cambial inactivity, and maturation, or lack thereof, of dw cells.

Suppose we draw radial lines across 1939 of XSC 1-1-b (text fig. 14), one passing through the left-hand letter C, another through the right-hand letter, C, and a third through the letter D₁. Then let us translate the structural features appearing along these lines into cambial activity. It is at once clear that the time of activity, the intervals of activity, and the rate of activity do not coincide either on the three radials taken together or on any two of them. After tracing the activity along various radials, we can more readily obtain a picture of general activity for 1939 over an area rather than on a cross section. Specimens such as XSC 1-1-b exhibit convincing evidence that cambial activity is not a simple process which begins necessarily with a burst of cell division in the spring, runs a regular course, declines, and finally ceases, not to be disturbed again until the following spring.

The section XSC 1-1-b (text figs. 15, 16) shows the increment for 1940 to be a system of compound and overlapping lenses, a half-lens, and two complete, entire growth layers. Actually two systems may be identified: that including growth layers 1 to 5 and that including growth layer 6 (text fig. 16). Growth layers 1, 1₁, and 2 entail all the problems already discussed in reference to half-lenses. Otherwise, lens 4 overlaps lens 3. Lenses 4 and 5 are a true compound lens wherein the outer, 5, covers the shorter arc (text fig. 1). It is interesting to note that, after the cambium indulged in activity of highly variable rate and location, 1 to 5, activity began everywhere on the cross section at about the same time, ran a uniform course apparently, and ceased everywhere at about the same time.

In connection with all the problems of variable cambial activity, the information from the Director of the Agricultural Experiment Station is to be recalled: the trees used in our work were not irrigated regularly after about 1936.

One more example is given from section XSC 1-2-b (text figs. 17, 18), showing increments for 1938 and a portion of 1939. The frosts for each year are shown at the start of each annual increment. Growth layer 1 (text fig. 18) is complete and entire. In contrast, growth layers 2 and 3 comprise a compound lens with the smaller lens on the outside (text fig. 1). At the midregion of the arc covered by growth layer 2, its outer margin is slightly indefinite. Here cambial activity had slowed down but not wholly ceased. In spite of this small region of indefiniteness, the fact that lens 3 covers less area than lens 2 indicates that lens 3 was made by a period of cambial activity distinct in a very real sense from that which made lens 2. The portion of the increment for 1939 shown in the drawing includes growth layers numbered 4-4₁-4₂, 5-5₁, and 6. Growth layer 6 is a simple lens. It is the

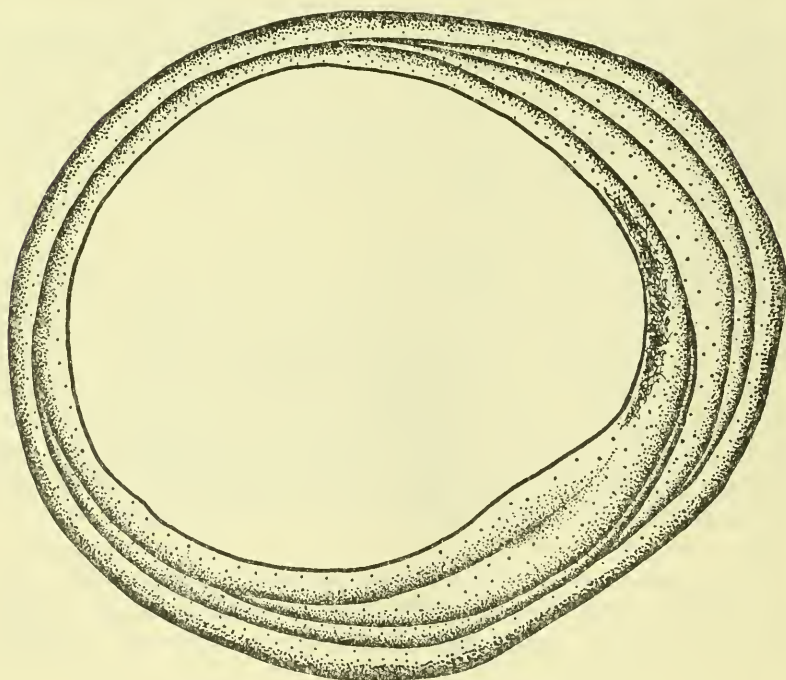
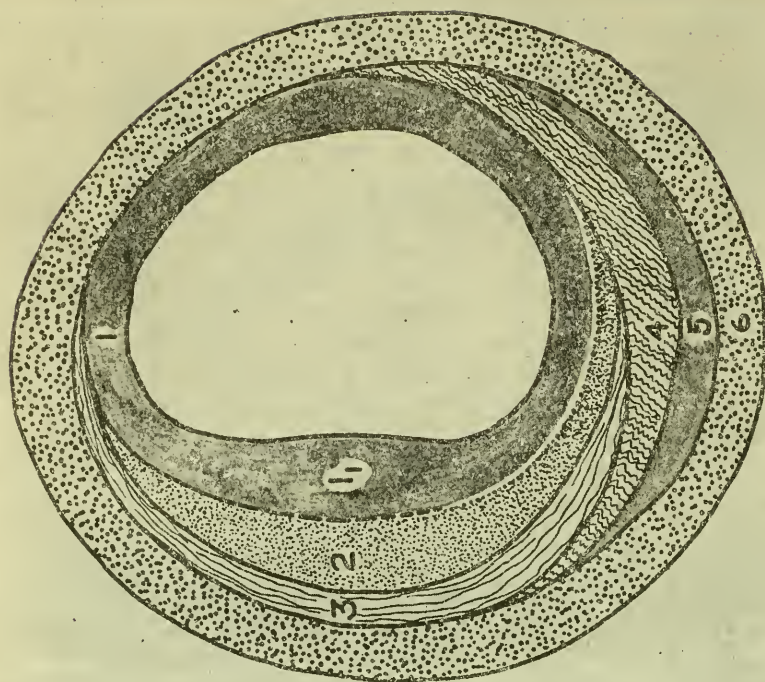


Fig. 15.—XSC 1-1-b. Increment for 1940. Multiplicity; complex system of overlapping and compound lenses; interpretation shown



1940

XSC 1-1-b

Fig. 16.—An interpretation of figure 15. Localized and periodic activity of growth processes. Contacts sharp, diffuse, or invisible. GIs are num-

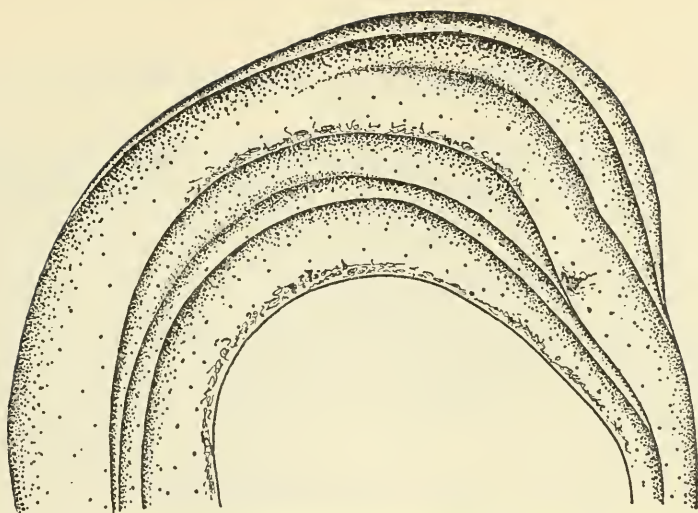


FIG. 17.—XSC 1-2-b. Increments for 1938-1939. Partial gls; variable long radius. Interpretation shown in figure 18. 1938: Effects of natural frost; sce; msL; sL; 1939: effects of natural frost; s $\frac{1}{2}$ L; sce; sL.

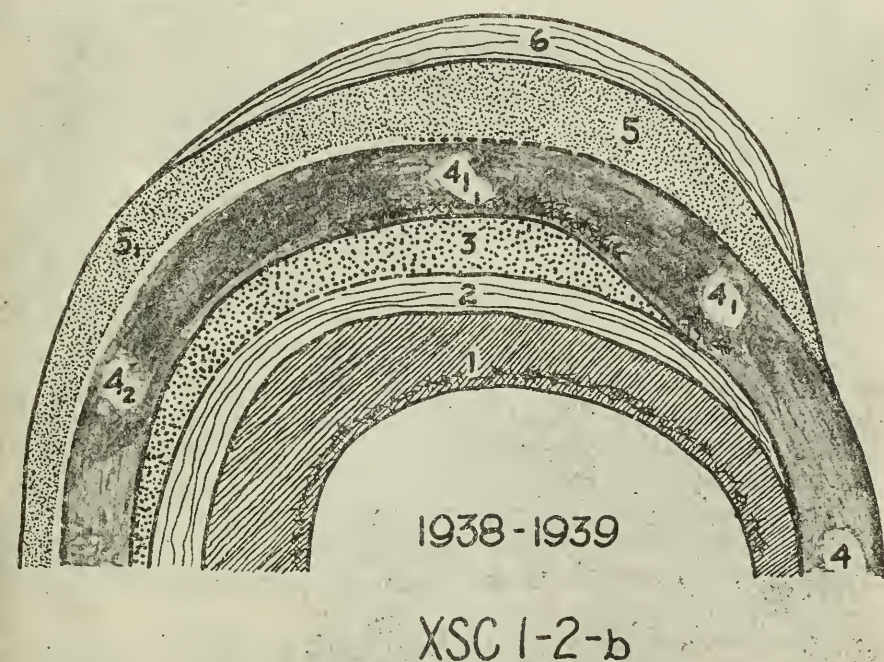


FIG. 18.—An interpretation of figure 17. Localized and periodic activity of growth processes. If contacts between gls are classified as sharp, diffuse, or "invisible," gl patterns are simplified and periods of activity (or flushes) are clarified. Gl's are numbered 1 to 6 to correspond to periods of growth activity. If the contact between 4 and 5 is interpreted as partly invisible (blank space, 4₂-5₁), then 4 becomes an entire gl and 5 an ordinary lens.

Interpretation of a contact as invisible suggests that growth activities can cease without wall thickening, heavy lignification, and failure to enlarge among the last formed cells. Lightwood is continuous across an invisible contact. By recognizing such a contact, half-lenses and arcs become understandable both physiologically and anatomically.

system 4 and 5 that brings up discussion. Previously, the portion 4_1 had been judged to be the half-lens. Now, the separate symbols for 4 and 5 suggest a system wherein $4-4_1-4_2$ is a complete, entire growth layer with an outer margin mostly sharp, partly diffuse, and partly invisible, and wherein $5-5_1$ is a partial growth layer, or lens, additive onto growth layer 4. Growth layer 5, in spite of the lack of densewood between 4_2 and 5_1 , represents an episode of cambial activity which tended to be distinct from the previous one but failed in structural evidence over a portion of the "contact." This adds a new interpretation to a half-lens and the cambial activity creating it (see also text figs. 14, 16, 18). How an understanding of cambial activity helps to clarify the classification of growth layers is well shown,

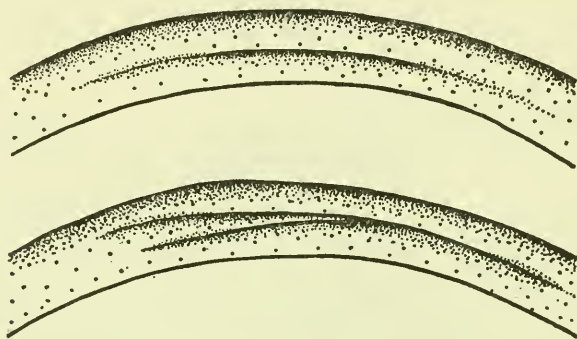


FIG. 19.—The simple and compound arc.

therefore, by comparing the figures just discussed with those which follow.

Temporary lenses by their nature cannot be static forms—they are transitional. Perhaps it is not too much to say that all lenses are temporary for a time. In any event, the term "temporary lens" may well be restricted to a locally stimulated area of the cambium such as out from the base of a twig or branch. All the work being reported upon here emphasizes the fact that cambial division begins locally, thence spreading outward tangentially and longitudinally. The rate, time, and universality of cambial division go far in determining the type of growth layer which results.

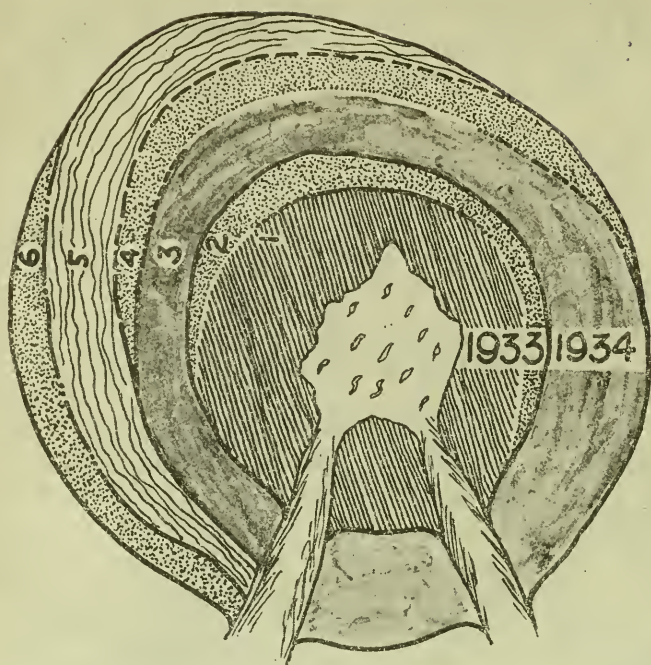
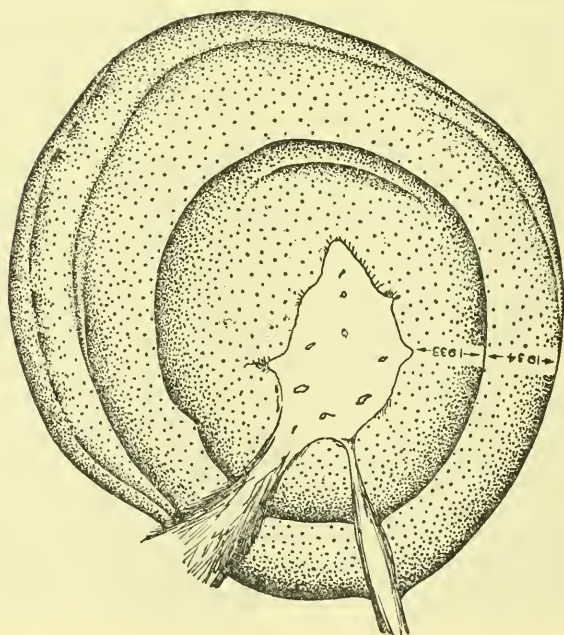
Arcs may be thought of structurally as lenses open at both ends (pls. 3, fig. 1; 16, fig. 1; 33). In reality, the growth layer is recognized on a cross section as a band of densewood with both ends "floating" free in lightwood. Text figure 19 shows a simple arc above and a compound arc below. The latter could, of course, be considered

a half-lens attached to a simple arc. Over total range, arcs vary from those with heavy densewood of sharp outer contact, to those of diffuse contact, and finally to those with densewood so feeble as to be almost invisible.

The arc as described is a feature seen in cross section. What occurs in longitudinal section? Two things are possible: first, the arc, as outlined by its densewood, actually "floats" free with no part of its densewood joining any other band of densewood; and second, the arc longitudinally changes into other growth-layer forms, partial and then perhaps entire.

An abundance of evidence supports the transition of arcs into half-lenses, lenses, and entire growth layers. Examples are plentiful but a few will be cited. In the 1940 increment of TTC 33-11, a sharp arc on sections *a* becomes a sharp, complete, entire growth layer on sections *b*, 12 cm. outward on the branch. In the 1937 increment of TTC 5-7, a sharp arc on sections *a* becomes a sharp lens on sections *b*, 33 cm. outward. In the 1936 increment of SA 6-1, a partly sharp, complete, entire growth layer on sections *a* becomes a sharp arc on sections *b*, 26.5 cm. outward. In the 1942 increment of Con T 2-7, a diffuse arc on sections *a* becomes a sharp, complete, entire growth layer on sections *b*, 7.7 cm. outward, and a diffuse, complete, entire growth layer on sections *c*, 1.4 cm. farther outward. In the 1940 increment of TTC 34-2, a diffuse arc on sections *a* becomes a sharp half-lens on sections *b*, 10 cm. outward, and back to a diffuse arc on sections *c*, 10 cm. farther outward. In the 1944 increment of TTP 20-40, a diffuse lens on sections *a* becomes a diffuse, complete, entire growth layer on sections *b*, 2 cm. outward, and a diffuse arc on sections *c*, 6 cm. farther outward; on sections *d*, 12.5 cm. outward from *c*, the arc has disappeared. Such examples could be multiplied, examples of arcs changing outward on the branch to half-lenses, lenses, or entire growth layers, or any of these changing outward to arcs.

Any treatment, any description of arcs seems so intimately bound up with the areal extent of the growth layer and with cambial activity that neither one can be discussed alone. Text figure 20 is a drawing of a cross section of a rather simple-appearing shrub *Althea* stem (see also pl. 3, fig. 1). As soon as we begin to visualize the stem in terms of cambial activity, text figure 21 seems to give the only logical result. With this interpretation, difficulties of identity disappear—the whole problem becomes a matter of cambial activity and the development of densewood. Thus, growth layer 1 (text fig. 21) assumes an identity as a "complete," entire growth layer whose densewood exists only over a portion of its circuit—in the vicinity of the branches and at the



arc. The contact elsewhere between growth layers 1 and 2 is invisible because densewood is absent. If it were not for the arc, we would have no means of knowing that the cambium experienced two episodes of activity during 1933 as represented on the cross section of SA 1-a. The methods used in the present work give us no clue to this interruption in cambial activity at the so-called invisible contact. In the future it is possible that either microchemical tests or examination under high power of cell walls on specially prepared sections will yield evidence for otherwise unknown interruptions in cambial activity. Growth layer 2, in continuation, becomes an exterior lens; growth layer 3 becomes a "complete," entire growth layer whose outer contact is partly sharp, partly diffuse, and partly invisible; growth layer 4 becomes a lens as indicated by the two facing half-lenses; growth layer 5 is a lens which partially overlaps growth layer 4; and growth layer 6 is a lens and, together with 4 and 5, makes a compound lens. In naming the features on text figure 20 (see also pl. 3, fig. 1), one becomes involved in what could perhaps be called the complexities of oversimplicity. For instance, exactly what constitutes the arc, the half-lens? These difficulties, although not made elementary by any means, largely disappear when the cross section is viewed as a product of cambial activity as set out in text figure 21.

Text figure 22 shows parts of the annual increments for 1938 and 1939, the frost spot at the left indicating the start of 1939. The figure, as well as the section itself, appears complicated at first sight, almost hopelessly so, especially on the actual specimen. However, if we set the above figure to a pattern, text figure 23, the complexities seem to fade to a great extent. The whole section includes for the most part entire growth layers and lenses, some simple and some compound, some sharp bordered and some diffuse. Growth layer 1 is a sharp lens, short and thick; growth layer 2 is complete and entire, partly sharp, partly diffuse; growth layer 3 is a long, sharp lens; growth layer 4 is a short, thin lens, partly sharp, partly diffuse; growth layer 5, a husky sharp-bordered lens, completely overlaps growth layer 4, and with growth layers 3 and 4 forms a compound overlapping and doubly overlapping lens system; growth layer 6 is a complete, entire growth layer, so far as the figure extends, whose presence is revealed solely by the arc of densewood; growth layer 7 is a sharp, complete, entire growth layer; growth layers 8 and 9 are a system of compound lenses. It is of interest to note here in passing that the visible densewood of growth layer 6 lies in the same circuit as the frost injury and undoubtedly is genetically related to low temperature.

Text figure 24, and text figures 25 and 27 with their accompanying

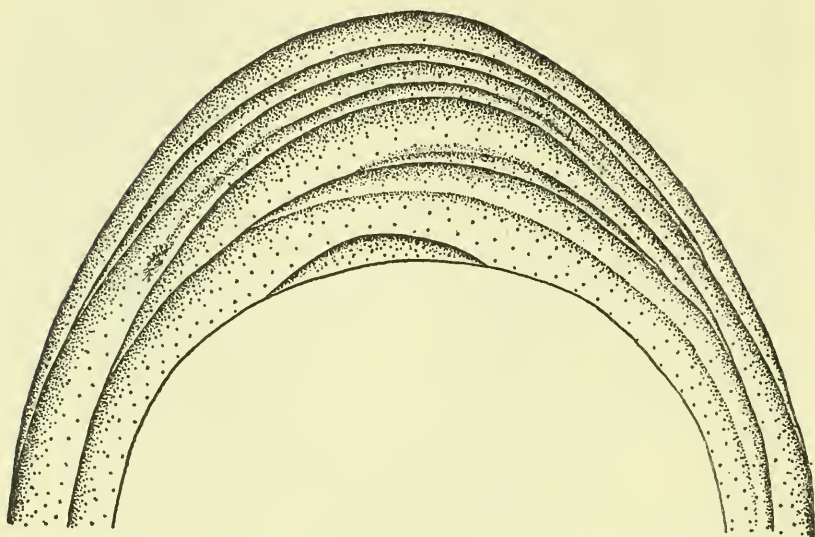


FIG. 22.—XSC 1-3-b. Increments for 1938-1939. Lensing; multiplicity in cambial and growth activities, and in gls. Interpretation shown in figure 23. 1938: sL; d $\frac{1}{2}$ L; sce; psL and sL, compound; 1939: spot of natural frost connected with an arc; sce; compound sL.

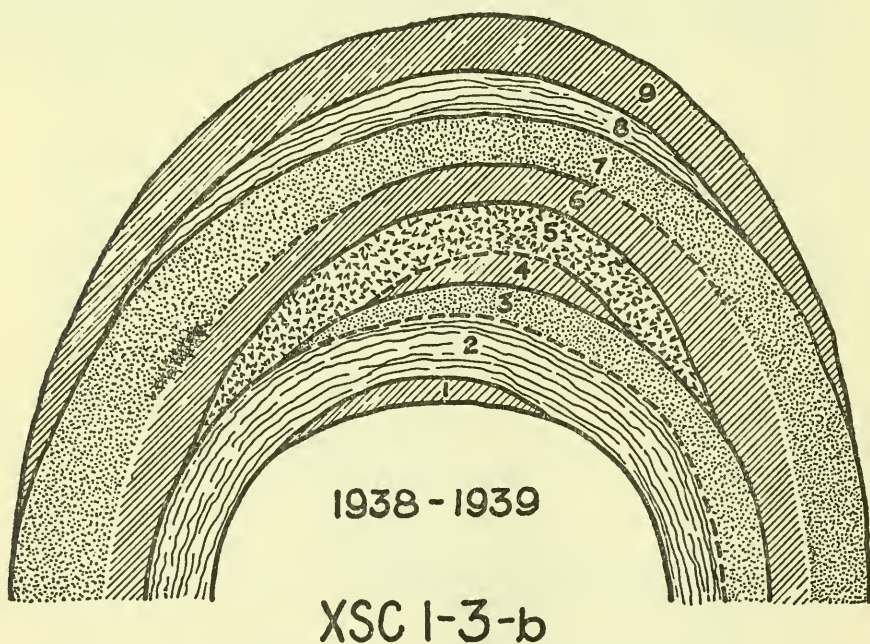


FIG. 23.—An interpretation of figure 22. Localized and periodic activity of growth processes. Contacts sharp, diffuse, or invisible. Gl's are numbered 1 to 9 to correspond to periods of growth activity. If the contact between 6 and 7 is interpreted as invisible at both extremities (blank spaces), then both 6 and 7 become entire gl's.

interpretations (text figs. 26 and 28), show increasing amounts of complexity all due to intermittent cambial activity.

A study of arcs, and particularly an attempt to delimit and classify them, focuses attention on the intermittency in time and space of cambial activity, and underlines the importance of a thorough study of growth fundamentals. Arcs whose densewood is entirely free floating in lightwood are theoretically possible, but complete proof would depend upon serial sections. We think that "free" arcs do exist,

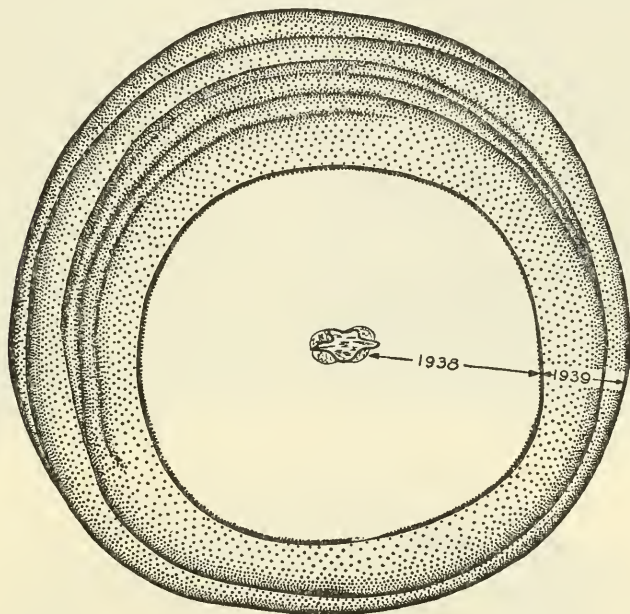
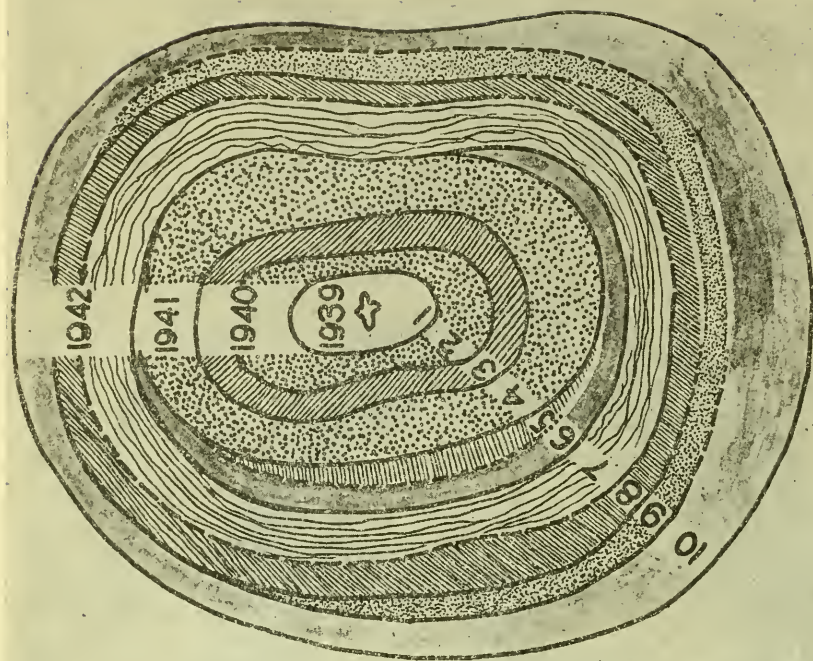
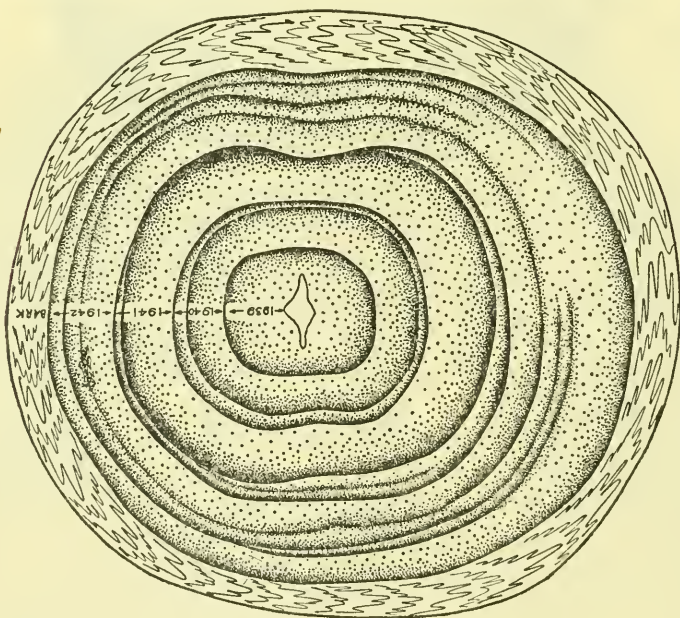


FIG. 24.—XSC 10-3-a. Increment for 1939. Complexity in one annual increment. Sequence: arc; msce; compound psL; msce; sL.

their densewoods in the shape of an open collar. Arcs whose densewood is not entirely free floating apparently are longitudinal projections from a cylinder of densewood, part of which is closed. From the evidence at hand, arcs may change into half-lenses, lenses, and entire growth layers.

A point to be emphasized is the wholly fallacious record given by one radius, and only one, taken anywhere on one of these sections which came from a tree grown under extreme lower forest-border conditions. Not only would the various radii disagree among themselves but also none would represent the section as a whole.



TTC 36-7-b

FIGS. 25 (left) and 26.—25, Increments for 1939-1942. Complexity of dated annual increments; compound arcs. Interpretation shown in figure 26. 1939: see; 1940: 2 see; 1941: see; long concurrent sL with d $\frac{1}{2}$ L; 1942: psce; long compound s arc; short d arc; see. 26, An interpretation of figure 25. Localized and periodic activity of growth processes. Contacts sharp, diffuse, or invisible. Gls are numbered 1 to 10 to correspond to the periods of gross activity. If the contact between 5 and 6 is interpreted as partly invisible (blank space after dw fades tangentially), then 5 becomes a lens, one member of the compound lens 5-6. Numbers 8 and 9 would classify as an

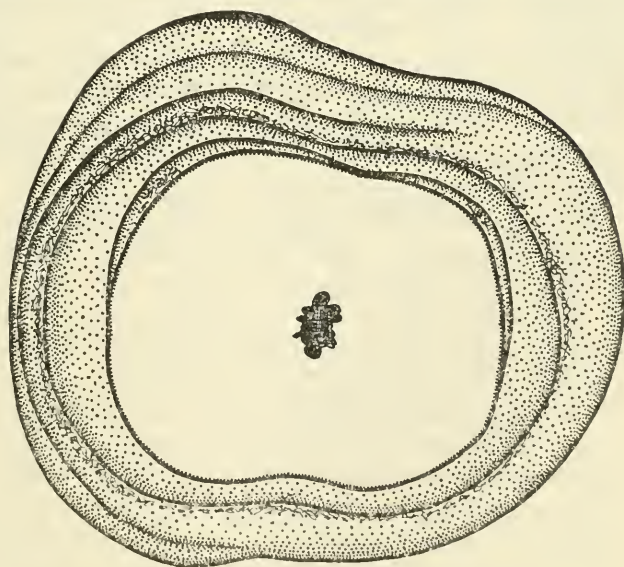
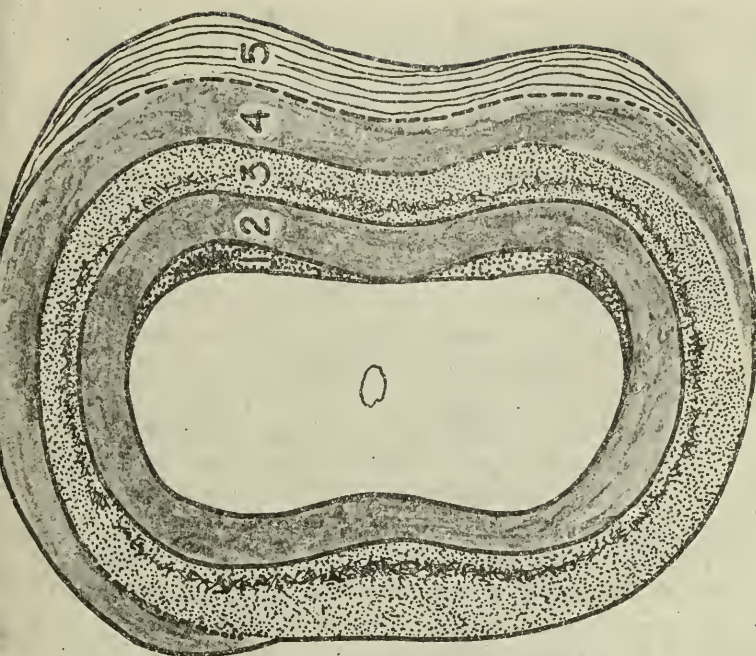


FIG. 27.—XSC 13-3-c. Increment for 1938. Two frosts and multiplicity in an annual increment. Interpretation shown in figure 28. Sequence: First frost in concurrent interior lens; second frost connected with scc; long s arc; psL; scc.



XSC 13-3-c

FIG. 28.—An interpretation of figure 27. Localized and periodic activity of growth processes. Contacts sharp, diffuse, or invisible. Gls are numbered 1 to 5 to correspond to periods of growth activity. If the contact between 3 and 4 is interpreted as invisible at both extremities of 4 (blank space), then 3 becomes an entire gl and 4 a partly sharp lens.

The term *divided densewood* is applied to that form of partial growth layer wherein the densewood, in its normal transition outward, is separated into two parts by the insertion of one or more tangential rows of lightwood cells. Text figure 29a gives an idealized but nonetheless accurate drawing. In a way, divided densewood has greater interest than the more clean-cut growth layers because it actually holds a transitional position in the array of partial growth layers (pls. 5, fig. 2; 10, fig. 1; 13; 19, fig. 2; 23, fig. 2; 25; 31, fig. 1).

Perhaps a description of one of our early encounters with the type will show how our attention was first attracted. In TTP 21-2-a, the increment for 1939 contains an exterior lens immersed for over three-quarters of its circuit in what would be called densewood under low magnification. Passing outward the sequence is as follows: About seven cells of decreasing width; one to three cells whose radial widths are greater than those immediately inward and outward; and last, one to four narrow cells completing the proper densewood transition and forming the outer part of the increment. Under low power the so-called lens appears to have an indefinite inner margin. This indefiniteness is not so much a matter of the feebleness of the outer margin of the inner band of narrow cells whose outer margin is actually very definite, as it is a lack of contrast between the narrow cells of the inner band of densewood and the slightly wider cells of the following lighter wood. This would bring physiological emphasis upon the impact of growth factors initiating or accelerating cambial activity, or maturation, after an interval of arrested or inhibited activity. In the case of TTP 21-2-a, the separation of the densewood into two parts may mean that growth-stimulating factors were actually feeble although still fluctuating in amplitude, or that growth factors were still operating on the tree but that the tree could not respond to the degree that it had earlier in the season.

Divided densewood undergoes various changes and transitions not only from branch to branch but also along a single branch. In tree TTC 33, and in other trees growing under much the same conditions, the bands of densewood have a tendency to separate into two or more bands, at some places the separation being barely apparent, at other places becoming a discrete lens or entire intra-annual growth layer.

The changes along a single branch are many and various. Complexity within an annual increment increases either inward or outward; divided densewood expands inward or outward into lenses or entire growth layers. Because of the nature of the xylem, our information is restricted to the gymnosperms. The following are a few of the examples of appearance and expansion inward: In the 1937

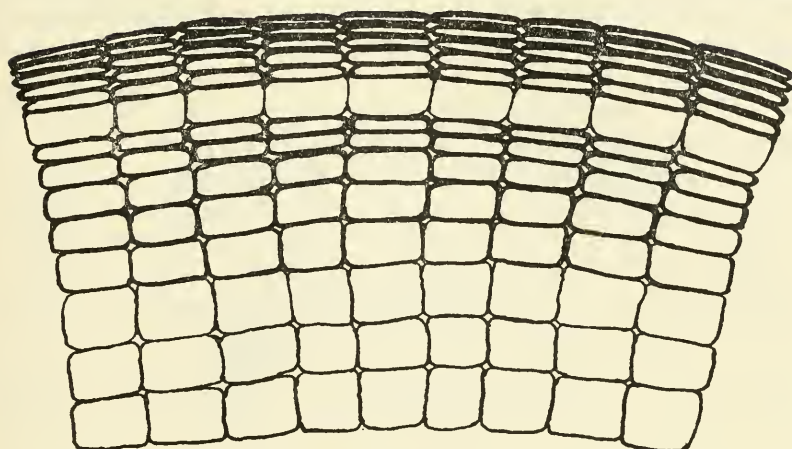


FIG. 29a.—Divided densewood (ddw) formed by the insertion of lightwood cells in the band of densewood.

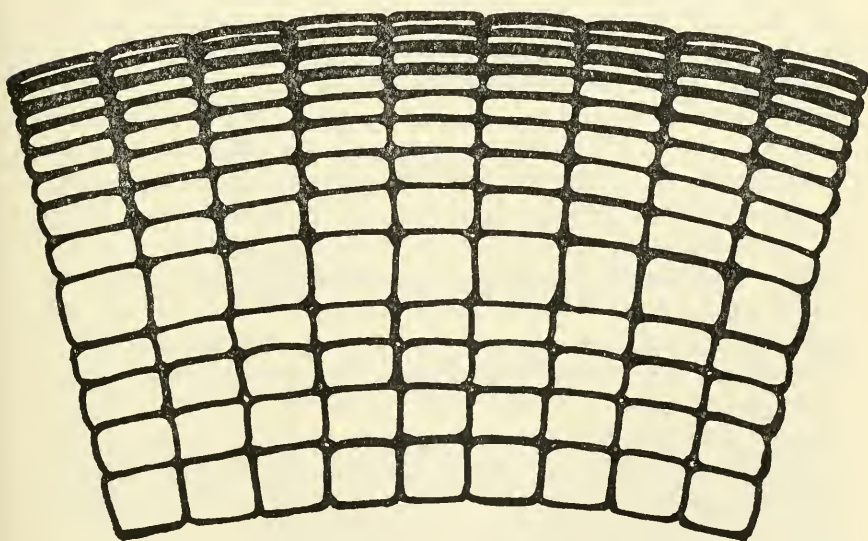


FIG. 29b.—Divided lightwood (dlw) formed by the insertion of extra thick cells in the lightwood zone.

increment of TTC 34-5, divided densewood is present in sections *a* and *b* (50.5 cm. and 42.5 cm. from the tip) but not in sections *c* and *d* (35.5 cm. and 27.5 cm. from the tip). In the 1939 increment of the same branch a complete, entire growth layer in sections *a* becomes a lens in *b* and *c* and divided densewood in *d*. In the 1941 increment of TTJ 2-12, sections *a* (46 cm.) contain a complete, entire growth layer, a lens, and concurrent divided densewood, whereas *b*, *c*, and *d* (35 cm., 33 cm., 22 cm.) contain only a complete, entire growth layer. In the 1939 increment of TTP 24-3, the complete, entire growth layer of *a*, *b*, and *c* (42, 35.5, 30 cm.) becomes divided densewood in *d* (20 cm.). In the 1940 increment of XSC 9-6, a complete, entire growth layer of *a* (52 cm.) becomes divided densewood in *b* (46 cm.) and remains so at least to within 29 cm. of the tip. In the 1938 increment of XSJf 1-1, divided densewood is present in *a* and *b* (65 and 50 cm.) but absent in *c* (36 cm.). In the 1938 increment of XSP 1-1, a lens of *a* (49 cm.) becomes divided densewood in *b* (33 cm.) and has disappeared outward by the time *c* (19 cm.) is reached. Equally vivid and numerous are the examples where complete, entire growth layers, or lenses, dwindle inward on the branch and ultimately disappear.

Interesting situations exist in some branches because the increment for one year has increasing complexity inward, whereas that of another year has increasing simplicity inward as if the years in any one branch were complementary to each other.

Divided densewood, if it is detected, can give a clue to the presence of a very weakly developed growth layer which otherwise would be considered to be nonexistent. In TTP 24-3-a the intimate contact of the densewoods of 1938 and 1939 and of the interior concurrent lenses of 1941 with the densewood of 1940 resemble closely what has been called divided densewood. At first, such densewood was thought to be of little importance. Later, it was found that divided densewood, and even undivided densewood, could represent two distinct growing seasons. The so-called invisible continuation of a lens around the circuit is revealed at places by a slight separation of the densewood where a row of wider tracheids breaks the normal outward sequence of progressively narrower cells. In certain instances, as TTP 24-3-a, the detection of an annual increment depends upon such slight evidence that it easily escapes notice. It is there, nonetheless.

The outer densewood of 1940, in TTC 33-11-a (text fig. 30; pl. 12, fig. 2), is multiple by the insertion of one or more rows of lightwood cells between the bands of densewood. In other words, the densewood of 1940 is made up of three bands over half the circuit and two over

the remainder. The divided densewood, or multiple densewood in this case, does not have contacts sufficiently sharp to warrant classification as lenses or intra-annual growth layers. It is rather a transition between multiple growth layers and a unified band of densewood.

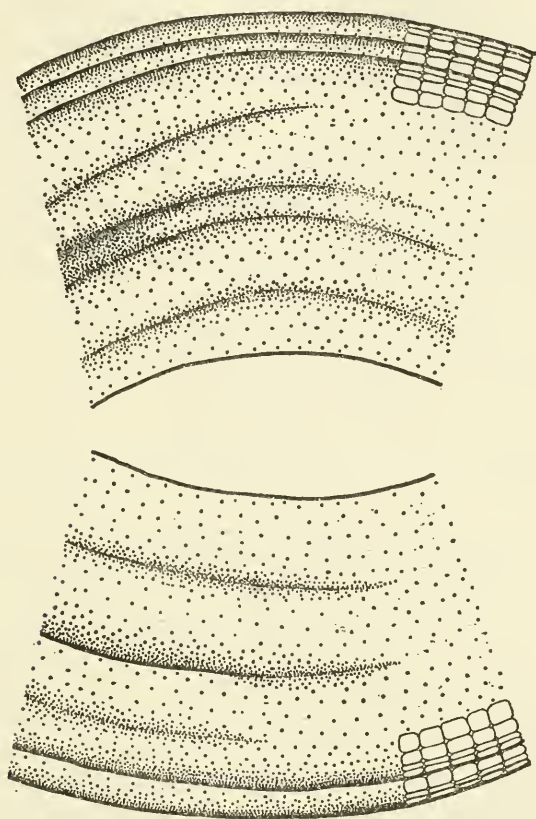


FIG. 30.—*TTC 33-11-a*. Doubly divided densewood (upper figure) in 1940 shown by symbol and cell structure, and fading of intra-annuals in the lightwood. Below, on opposite radius, singly divided densewood.

Such terms as “indistinguishable growth layer” and “low-power” lens may be misleading to be sure, but they serve a useful purpose in emphasizing the complexities, both structural and physiological. To all appearances, the increment for 1940 in *TTP 23-4-a* is absent around the circuit except in two places where it reveals itself under high power as part of divided densewood of 1939 and as composed of one or two wider cells and one or two narrower cells. This instance comes closest of any in our collection to being a totally absent growth

layer (on one cross section, of course). As indicated, however, the detection of 1940 is not too difficult and, in all probability, it is represented around the entire circuit, being reduced at its minimum to one row of densewood cells. The eye can follow this continuity. Constant encounters with growth layers, such as the one for 1940 above, makes one doubt that normal cambium can successfully refrain from cell division throughout an entire growing season. In the other branches of tree TTP 23, the increment for 1940 is highly variable in width, and present either as an entire growth layer or as a lens whose densewood forms part of a band continuous around the circuit. Therefore, in TTP 23-4-a, 1940 is simply reduced to a minimum—reduced to such an extent that its presence could easily pass undetected. The outer portions of the branch (TTP 23-4-b and c) show 1940 much more completely developed, and thus its presence as described in TTP 23-4-a is substantiated. The highly variable thickness of the 1940 increment, not only among different branches of TTP 23 but also along the extent of a single branch, would make a calculation of 1940 volume increment decidedly uncertain and could vitiate or destroy the value of any correlations between rainfall and 1940 tree growth. Even the average thickness on one entire cross section, not to mention a single radius, is apt to give a highly erroneous measure of thickness for the 1940 increment as a sheath over the entire plant body.

The inner group of the 1933 increment in XSC 1-2-b consists of a thick, entire growth layer, a long exterior lens, and divided densewood. Near one cusp of the lens, the densewood of the main growth layer is divided into three narrow bands whose resolution depends upon the use of high power. The outermost band of narrow cells in the multiple divided densewood grades laterally into wider and wider cells which become part of the lightwood at the start of the outer group of growth layers in 1933. Therefore, it is a half-lens which begins as divided densewood of an inner growth layer and becomes a half-lens in the early part of the next outer growth layer. That the site of a lens is a place where high local stimulation affects the cambium is illustrated not only by full compound lenses but also by the less accentuated compounding in which apparently the outer of the lenses is developed merely to the extent of divided densewood of the inner lens, as in the increment for 1934 of XSC 1-1-b.

Amount of magnification is an important factor in the detection of growth layers, in their classification, and in their interpretation as regards cambial activity. So-called "low-power" lenses, divided densewood, and entire growth layers lacking lightwood over much of the circuit are so closely related they seem to be part of the same feature.

This is amply illustrated by the increments for 1939 and 1940 in TTP 21-6-a, for 1939 and 1940 in TTP 21-8-a, for 1940 in TTP 21-8-b, and for 1940 in TTP 23-3-a. Under low power, 1939 and 1940 appear to be very weakly developed lenses (actually divided densewood) of one or several concurrent members. High power shows that it is only the lightwood which is lenticular, the densewood being continuous around the circuit. The entire band of densewood may be reduced at places to a thickness of one cell only. In fact, continuous tracing under high power indicates that the combined bands of densewood for 1939 and 1940 at one spot in TTP 23-3-a are reduced to a thickness of two narrow cells. More than this, in TTP 23-1-a, the densewoods of 1941 and 1940 lie against that of 1939 (see pl. 19, fig. 1). No evidence has come to light throughout the complete range of the work to suggest that the cambium failed to divide during a single season.

The above examples do not show the most extreme cases of incipient cambial activity. A study of the rather wide densewoods, as well as the compression zones, of XSC 1-5-b, reveals many detailed alternations of narrow and wide cells. Do these show high sensitivity to slight fluctuations of physiological activity or repressed indications of the impact of rather intense fluctuations? The very beginnings of divided densewood are shown in the broad band of 1937 densewood of TTP 20-6-a which is made up of successive alternations of radially narrow and wide cells. Here again sensitivity appears to have been high, giving a rapid alternation of conditions so slightly recorded in the xylem.

Some evidence exists for the presence of what could be called *divided lightwood* (text fig. 29b). Halfway out in the 1941 increment of Con T 2-9-a, a zone of wide cells encircles the section and may record accelerated growth at the start of the second 1941 tip flush (see 1933 in pl. 2, fig. 2). On the long radius and confined to the compression wood, the increment for 1942 in Con T 2-6-a gives evidence of three diameter flushes: one-third and two-thirds of the way out there are rows of wider cells. These seem to be a rather delicate test for the presence of factors periodically causing accelerated diameter growth, more delicate at least than tip growth of which there were two flushes in 1942.

Divided densewood and divided lightwood, as transitional forms and as indications of cambial activity, are perhaps not only the most interesting but also the most suggestive forms of partial growth layers.

The term *interrupted densewood* is applied to that form of partial growth layer wherein the densewood, in its normally progressive

transition outward, is separated into two parts by the insertion of one or more tangential rows of densewood cells narrower than those immediately to the interior and exterior (pls. 16, fig. 2; 18, fig. 1). In other words, the normal outward transition from typical lightwood to the growth-layer boundary is interrupted by the narrower cells as shown in text figure 31a and plate 19, figure 3.

What interrupted densewood means physiologically is not clear. Cell enlargement stops suddenly and maturation appears to have a concentrated effect. In any event, the factors permitting growth were given a sudden but temporary check.

Inward some 12 cells from the outside of the 1940 growth layer in TTP 24-17-a, there is an arc of narrow cells coming as an interruption to the normal succession of densewood cells. The arc has become an entire circle in sections *b*. In the 1940 increment of TTP 24-16-a, 47 cm. from the tip of the branch, several arcs of narrow cells exist; in sections *b*, 35 cm. from tip, and in sections *c*, 26.5 cm. from tip, the arc of narrow cells has lengthened into a band extending completely around the circuit as interrupted densewood. These examples could, of course, be multiplied.

The densewood of angiosperms appears to be marked by intermittency; that is to say, the densewood exists as patches, the gaps being filled with tracheids typical of lightwood. Whether the densewood belongs to an annual or to an intra-annual makes no difference. Silver maple and Siberian elm, among the angiosperms used in our work, show these gaps as a common feature.

This sudden insertion of cells which failed to enlarge but are "over-matured" relative to their immediate surroundings may, as a matter of fact, occur anywhere throughout a growth layer and, if within the compass of the lightwood, they are termed *interrupted lightwood* (text fig. 31b; pls. 2, fig. 3; 3, fig. 2; 10; 11, fig. 2). These cells may be disposed as circles, arcs, patches, and isolated cases of abnormally narrow, thick-walled cells in one or two rows. Certain angiosperms are especially prone to such. Cross sections of the Siberian elm habitually possess arcs, stringers, bands, and patches of narrow cells. All growth layers of TTE 1-1-a, for instance, have stringers of narrow rectangular cells which contrast strikingly with the irregular polygonal tracheids elsewhere in the growth layers. These cells cannot be distinguished from ordinary narrow cells of densewood. The sections of TTE 1-2-a give many hints of lenses that cannot be sharply delimited. High magnifications obscure general relationships, and very low magnifications mask cell contrasts.

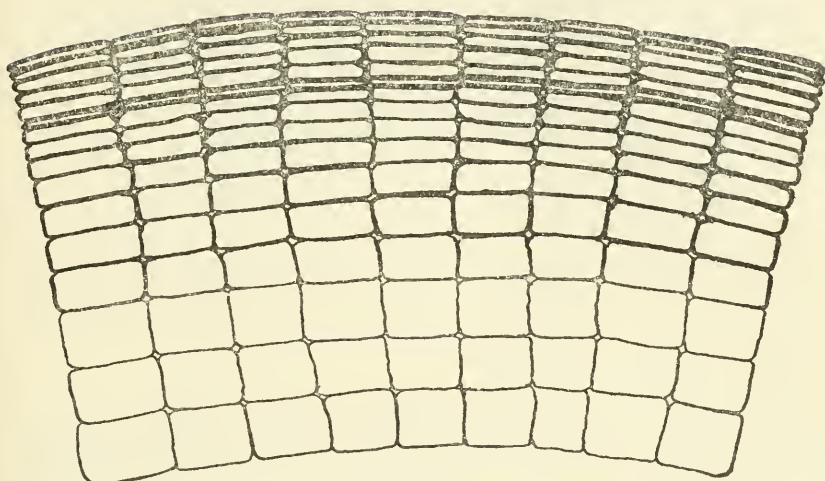


FIG. 31a.—Interrupted densewood (idw) formed by the insertion of extremely thin densewood cells in the band of densewood thus interrupting the normal transition outward.

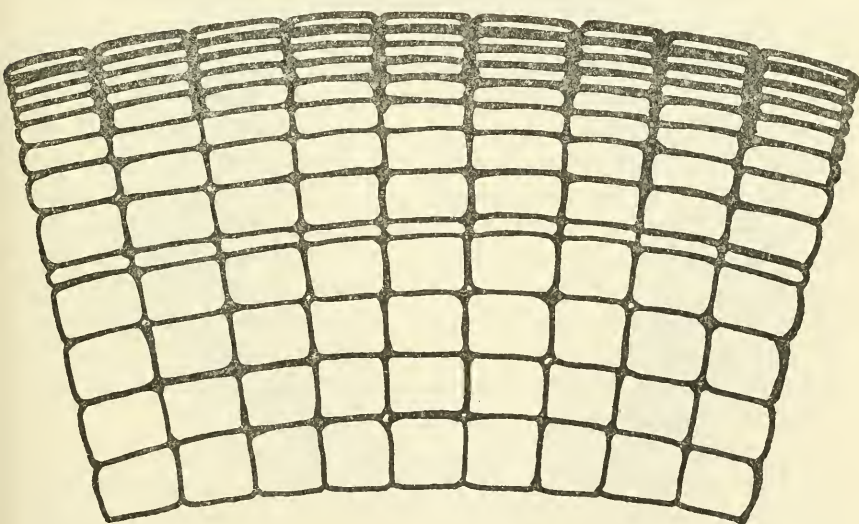


FIG. 31b.—Interrupted lightwood (ilw) formed by insertion of extra thin cells in the lightwood zone.

Many of the same features made up of densewood cells exist in gymnosperms, in normal lightwood, and in compression wood. Their common presence in compression wood seems to give a highly sensitive indication of fluctuating growth conditions. Furthermore, rhythmic alternations by a multiple succession of arcs and complete circles of narrow cells appear to characterize the xylem in certain trees. Hence, all degrees of growth slowdown or even of cessation appear to exist on one radius, on several radii, or even entirely around the circuit. The 1938 increment of TTC 30-1-a contains arcs and lenses of densewood and compression wood plus several zones of narrow cells, so that the growth layer appears to have had rhythmic growth throughout the season. Also, the growth layer contains an alternation of compression wood and lightwood which is not necessarily coincident with the bands of narrow cells.

The term *curtain*, or *densewood curtain*, refers to a zone of densewood, or of highly lignified cells, at the start of a growth layer which, therefore, does not have the simple, normal sequence of lightwood and densewood (text figs. 32, 33; pls. 1, fig. 2; 9). The lightwood of the growth layer follows the curtain outward radially. In constitution, the curtain may be either a band of uniform densewood cells within the range of uniformity applied to densewood, or it may have variations in thickness of wall and in width of lumen. These variations may be radial or tangential in the same curtain. Followed tangentially, the typical definite outer margin of a curtain may become either a sharp or diffuse band of densewood or the curtain may either disappear or change into a genuine growth layer with a threadlike densewood. A curtain may disappear by changing laterally into normal lightwood. Again, it may disappear by its outer portion becoming typical densewood with a sharp margin and its inner portion becoming lightwood; thus the curtain changes laterally into a sharp-margined intra-annual growth layer. On the same circuit and within the same annual increment, a curtain may show all phases. Growth-layer interpretations, based upon individual radii from several places on a section, would be hard pressed indeed for an explanation of the variation among the radii in absence of the complete section.

The curtains we have encountered occur almost exclusively in the Arizona cypresses from the grounds of the Texas Agricultural Experiment Substation. In XSC 3-1-b the increment for 1935 contains five complete, entire growth layers, the fourth of which has, at the start, a curtain of cells considerably narrower and more heavily lignified than those immediately to the exterior (text fig. 32). The complete growth layer, in fact, appears to possess a two-way radial

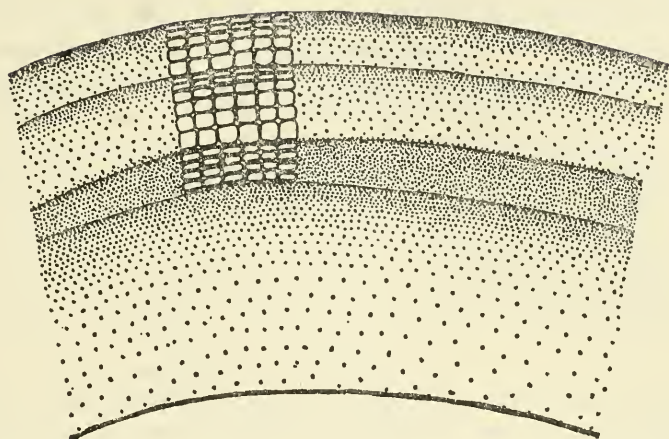


FIG. 32.—XSC 3-1-b. The increment for 1935 in symbol and cell structure. Multiplicity and a midincrement curtain. Sequence shows: sce followed by dw curtain; 2 sce.

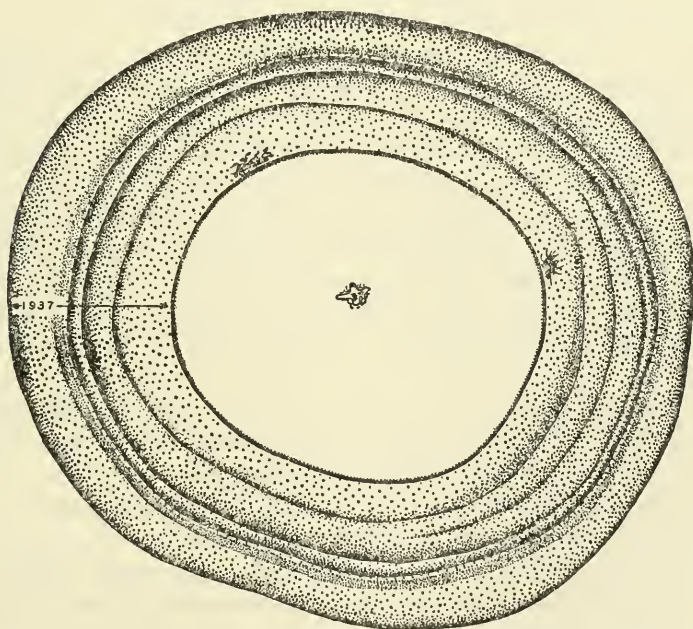


FIG. 33.—TTC 12-9-b. Increment for 1937. Multiplicity; arc; curtain. Sequence: Spots of natural frost; psce; s arc; msce; sce and msce curtain; sce.

sequence, the lightwood being in the center and densewood lying both interior and exterior to it. No curtain recognizable as such exists in sections *a*, 17 cm. inward, or in section *c*, 15 cm. outward from *b*. Either it is entirely absent from these sections or it is represented by some other type of growth layer. Perhaps the most interesting situation exists in the increments for 1934-1935 of XSC 6-2. The sections for XSC 6-2-a, 117 cm. from the tip of the branch, show two curtains, one of which could actually, and perhaps more logically, be interpreted as two thin, sharp, complete, entire growth layers, and the other of which changes laterally into a sharp lens (as does the curtain at start of 1939 (pl. 1, fig. 2). These curtain effects are even more conspicuous in sections *b*, 100 cm. from the tip, and are excellently developed in *c*, 85 cm. from the tip. In fact, XSC 6-2 is remarkable not alone for its curtains but also for its multiplicity; for its concurrent lenses; for a narrow, weak, "outer" growth layer which constitutes the outermost growth layer of a multiple annual increment; for thin densewood bands one cell in thickness; and for multiple divided densewoods. The increment for 1935 in XSC 6-3-a contains two curtain growth layers. One of these changes laterally into a growth layer with multiple densewood which, in turn, becomes a sharp lens.

The conditions present when a curtain is formed must resemble those present when densewood is formed—inhibited cell enlargement, accentuated cell maturation, and increased deposition of tannins, resins, and lignin. During the formation of a curtain, then, these conditions are present at the start of growth-layer formation as well as at the close. One wonders if the rate of cambial activity is less than for normal lightwood. In XSC 2-2-c, the curtain in 1938 is definitely related to late-spring frost injury which indicates restricted cambial activity. Not the frost effects, particularly, but the restricted cambial activity may be highly suggestive as to the reason for the existence of curtains.

The presence of curtains, of course, detracts from the sharpness of the growth-layer boundary against which it lies. This is increasingly true, the lower the power of magnification used.

In some instances, curtains could be more accurately classed as complete growth layers than as partial growth layers.

Postseasonal growth as a term is applied to any growth which produces an incomplete growth layer, however restricted, after the major growth flush (or flushes) has been completed. The formation of post-seasonal growth may occur, theoretically and practically, at any time during the calendar year except for that part of the growing season which is the chief period when diameter growth occurs. Of course, it

is impossible to foretell if added growth found during the summer would have gone on to completion. Evidence does exist for the addition of added xylem after the main flush is completed and before the arrival of winter. Therefore, descriptions are based chiefly upon sections cut during the winter.

Postseasonal growth may be divided into three types: (1) Tracheids or vessels added outside the normal and sharply bounded outer growth layer—that is, isolated cells or groups of cells (pls. 10; 11, figs. 1 and 2; 17, fig. 1; 19, fig. 1; 30, fig. 2; 32); (2) incomplete maturation of the densewood of the outer growth layer (pls. 16, fig. 2; 17, fig. 1; 19, fig. 1; 33); and (3) transition outward of the outer densewood into cells approaching the character of lightwood (pls. 11, fig. 3; 12, fig. 1).

The first type may exist as isolated individual cells, as patches or crude lenses, or as distinct but incomplete lenses and entire growth layers. In the juniper, TTJ 1-1, cut January 11, 1940, sections *a*, 80 cm. from the tip, carry scattered single immature cells under the cambium. Sections *b*, at 61 cm., and *c*, at 44.5 cm., duplicate the situation in *a*. At 24 cm. from the tip, sections *d* show the merest hint of added xylem with one or two very immature cells. Specimen TTJ 2-1 practically repeats TTJ 1-1.

During 1940 a series of branches was cut from the Arizona cypress, TTC 5, at approximately 2-week intervals. No extra xylem had been formed by July 17 when specimen TTC 5-4 was taken. In sections *b* of TTC 5-5, cut August 1, one or two cells had appeared. In TTC 5-6-a, cut August 17, postseasonal growth consists of a 100° incomplete lens one to two cells thick. Sections *b* show the long lens of *a* broken down into a series of short, thin, incomplete lenses. In TTC 5-7-a, cut September 10, a cell or two gives the merest hint of post-seasonal growth. Sections *b*, 33 cm. closer to the tip, show two small lenses, one cell thick, of immature cells. In TTC 5-8-a, cut September 28, 72 cm. from the tip, extra xylem exists as scattered cells and one or two short lenses of immature cells. Sections *b*, 14 cm. from the tip, show a cell or two of added xylem. TTC 5-9, cut November 9 and showing added xylem, indicates that the postseasonal growth which began to be formed soon after July 17 actually was put down as, and remained, postseasonal growth.

Many examples exist of added xylem present in midsummer, but without sections taken at stated time intervals, no information exists as to whether or not the added growth would have remained such or gone to completion. Practically all our evidence indicates that diameter growth is essentially completed by mid-July; anything present on

the exterior of the completed growth layers remains as postseasonal growth. For instance, TTC 12-12 was sectioned on July 31, 1944. Sections *a*, 23 cm. from the tip, possess for 1944 two sharp, complete, entire growth layers and a hint of added xylem on the long radius. Sections *b* (pl. 10, fig. 1), 14 cm. from the tip, possess for 1944 two sharp, complete, entire growth layers, a sharp lens, and a diffuse lens in addition to several lenses of immature xylem one cell thick. Sections *c*, 2.5 cm. from the tip, have for 1944 two sharp, complete, entire growth layers plus single cells scattered around the circuit. Such added growth is a phenomenon not at all uncommon on branches sectioned in midsummer, either on gymnosperms or angiosperms.

Much additional information has been obtained from sections taken along a branch. A series of branches, TTP 24-13 to 24-15 and 24-23 to 24-25, was cut January 1, 1943. Two representative specimens will illustrate the series. In TTP 24-13-a, 53 cm. from the tip, the increment for 1942 contains one sharp, complete, entire growth layer, divided densewood, and added xylem of thin concurrent lenses composed of one to two rows of immature cells. Sections *b*, 41.5 cm. from the tip, contain one sharp, complete, entire growth layer, a diffuse lens, and many narrow lenses of immature cells extending in a series almost continuous around the circuit. Sections *c*, 30 cm. from the tip, contain the same sequence for 1942 as *b* except for the lack of postseasonal growth. In TTP 24-24-a, 15 cm. from the tip, the increment for 1942 contains one sharp, complete, entire growth layer. Sections *b*, 9.5 cm. from the tip, and *c*, 6.3 cm. from tip, contain, in addition to one sharp, complete, entire growth layer, postseasonal growth of several concurrent lenses composed of one or two rows of immature cells. Sections *d*, 0.3 cm. from the tip, show merely slight evidence of added growth.

There remain, in the discussion of the present type of postseasonal growth, three examples of special interest. The so-called Conservatory trees were moved indoors November 16, 1939, from the grounds of the Experiment Substation. Tip growth appeared to be in progress to a slight extent on November 29. As regards the sections cut on that date, there was no doubt that the trees were laying down cells of postseasonal growth. Specimens of the different trees, Arizona cypress (Con C), ponderosa pine (Con P), and loblolly pine (Con T), agree in showing added xylem of isolated cells, incomplete concurrent lenses, or an incomplete, entire growth layer. After a short time we came to look for the "Conservatory growth layer" because it was so characteristic of all specimens, no matter whether they were cut in late 1939 or any time up to 1945. The evidence indicated that the trees were stimulated into growth by removal to the Conservatory and that there

they grew various amounts of xylem which we called the Conservatory growth layer.

The second example included a group of seven branches cut off February 21, 1942. The three weeks prior to the week of cutting had been unseasonably warm and had had one slight rain. In all sections taken from the branches, the cambium was in excellent condition. TTC 33-8 shows no growth which could be associated with the warm spell. In TTCw 1-4 the cambium had just begun activity and constituted a zone, three to four cells thick, rich in protoplasmic contents. In TTE 2-4 an active cambium had just set off immature vessels and tracheids. The cambium in TTL 3-5 may possibly have been active; that of TTM 1-5 was likewise questionable. TTP 20-17, *a*, *b*, and *c*, shows scattered cells of postseasonal growth in addition to an excellent cambial zone made up of large cells, three to four rows thick radially. Only a much-expanded bud revealed the effect of warm weather on TTP 24-9.

The third example concerns specimens from citrus trees grown on the Experimental Farm at Yuma, Ariz. In all branches, growth was actively in progress on November 26, 1940. The presence of vessels and tracheids in some branches suggests rather rapid growth. The climatic regime at Yuma is, of course, different from that at Lubbock, Tex., and apparently growth occurs during the winter. According to the Superintendent of the Farm, tip growth occurs after each irrigation.

The second type of postseasonal growth—incomplete maturation of the densewood of the outer growth layer—does not occur so commonly as the first type. Also, it is less easily detected. Some question may be raised as to the propriety of referring to immature densewood as postseasonal growth. If wall thickening and lignification occur after the normal season of growth, even during the following season, then we seem justified in calling the processes and the resulting materials postseasonal growth. The specimen TTC 30-2 was cut December 15, 1939. In sections *a*, 67 cm. from tip, the increment for 1939 contains one mostly sharp, complete, entire growth layer and one incomplete, entire growth layer. The outer growth layer of 1939 does not have a sharp outer contact, and the outer cells of the densewood are partially immature in that the walls are thin and unlignified. At the time of cutting, growth was not complete as shown by the immature cells; the growth layer itself was not complete as shown by its indefinite outer contact. It may be worthwhile to point out that the margins of 1937 and 1938 bear an indefiniteness quite similar to that of 1939. Perhaps the circumstances surrounding the formation of the

postseasonal growth of 1939 throw light on the conditions during the formation of 1937 and 1938 growth layers. In sections *b* of TTC 30-2, 46.5 cm. from the tip, the evidence for postseasonal growth is less accentuated. In sections *c*, 32.5 cm. from the tip, and sections *d*, 18.5 cm. from the tip, the 1939 increment is composed of xylem mature outward to its sharp margin.

The third type of postseasonal growth does not show a failure to complete a growth layer in the season to which it rightly belongs, but rather a transition outward from the outer densewood into cells which can only be classed as lightwood. These cells are, in the main, larger, thinner walled, and less heavily lignified than the cells immediately to their interior. If this thin zone of transition were examined some years later, rather than when examined originally, the examiner would be in a quandary not only as to the actual identity of the annual increment but also as to the exact boundary between 1939 and 1940.

Con T 1-18 (sections *a*, 4.6 cm. from tip, and sections *b*, 0.2 cm. from tip) was sectioned January 16, 1943. For a short distance along the outer margin of 1942, the outer three or four rows of cells become larger and thinner walled, perhaps correlating in part with a second tip flush.

TTC 5-9-a, cut November 9, 1940, 69 cm. from the tip, bears a slight hint of added immature cells; sections *b*, 34 cm. from the tip, have no added xylem. On February 1, 1941, a neighboring branch, TTC 5-10, was cut and sectioned. It shows no postseasonal growth. Other branches, cut at 6-week intervals, did not permit identification of the prior postseasonal growth. If once present, it had been incorporated into the next year's growth. TTP 20-1 reverses the sequence of TTC 5-9 as regards change along the branch. Sections *a* of TTP 20-1, cut November 26, 1939, 37 cm. from the tip, have one sharp, complete, entire growth layer for 1939, whereas sections *b*, 5 cm. from the tip, have one sharp, complete, entire growth layer plus one diffuse lens and postseasonal growth whose cells were larger than the normal densewood to the interior.

Many specimens of XSC show excellent postseasonal growth but they are not cited as examples because all of them were subjected to artificial freezing and hence may have had their normal course of growth interrupted.

The increment for 1939, in TTC 30-1 (pl. 11, fig. 3), cut November 4, 1939, consists of one incomplete growth layer. Apparently growth was in progress on the date of cutting. In the zone of compression wood, no narrowing of cells is detectable; away from the compression wood, some cells have become narrower but they are followed outward

by larger, thinner-walled, green cells. TTC 30-1 combines two types of postseasonal growth.

In summary, the evidence from a study of postseasonal growth makes it quite clear that a growth layer, even though it be a circle on a cross section, is not necessarily a simple affair; that tree growth is not restricted to a single pulsation during any one season, or year; and that all the xylem of a growth layer when studied later may not have been formed at the same time as the chief portion of the growth layer. Actual xylem may have been placed at a later date or the growth processess may have gone to completion later than supposed. Computation of the precise amount of xylem formed in the year succeeding the formation of the postseasonal growth would be in error by the amount of that growth, and the thickness of the xylem would yield exaggerated results if compared directly to growth factors operating in the year or portion thereof following the formation of the postseasonal growth.

Some evidence exists to suggest that on occasion the laying down of postseasonal growth is accompanied by terminal bud expansion or even bud elongation. Of the specimens heretofore mentioned, Con T 1-18 and those cut off Feburary 21, 1942, bear out the probable correlation of the attempted simultaneous growth in diameter and in length.

SUMMARY OF CLASSIFICATION AND TYPES

LONGITUDINAL VARIATIONS

A classification of growth layers such as here outlined actually represents a synoptic view taken at one locality in a branch at one particular time. Without doubt, growth layers pass from one type to another longitudinally along the branches. A lens may become an entire growth layer; divided densewood may become a lens and then an entire growth layer; an arc may become a half-lens, then a lens, and finally an entire growth layer; or vice versa. Lenses may be partially cylindrical "patches," as it were, or an entire growth layer may project longitudinally as several "fingers," a cross section of which would show the "fingers" as a concurrent lens system. Arcs can be represented by densewood as "floating" in lightwood, or along part of its edge the densewood may join an adjacent band of densewood giving, in cross section, a half-lens. The free edge of a half-lens may drift over to unite completely with adjacent densewood, thus giving a lens in cross section. Text figures 34 and 35 show how the position of the section determines the nature of the growth-layer sequence and how growth layers change from one type to another longitudinally.

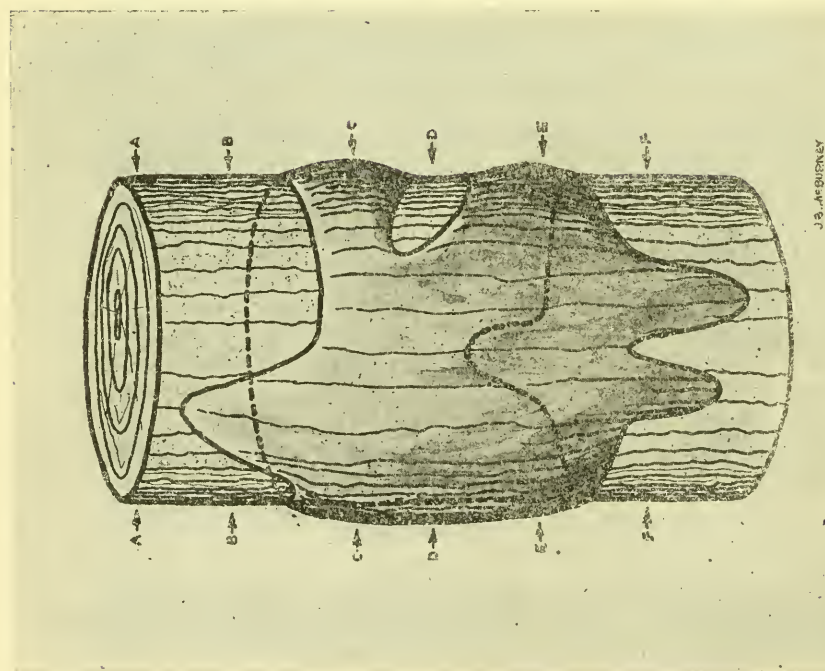


FIG. 34.—Diagram constructed to show possible areal distribution of growth patterns on different parts of a tree trunk. These locations where growth did not occur are not necessarily the same as those shown in the photograph.

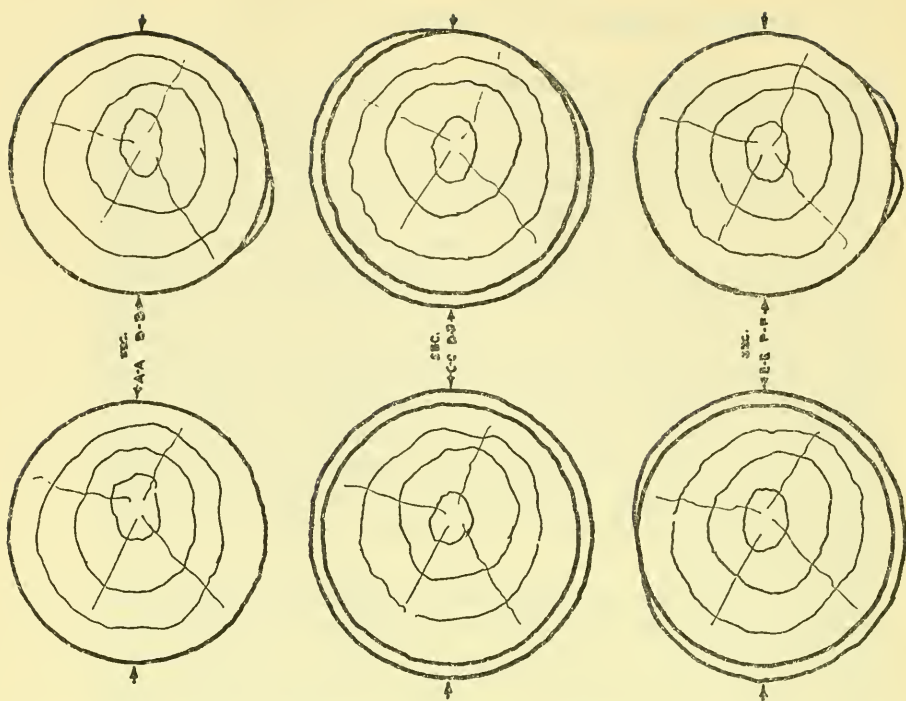


FIG. 35.—Transverse sections taken at the lettered arrows on Figure 34. These locations where growth did not occur are not necessarily the same as those shown in the photograph.

These are a few of the types of growth layers as they actually exist in the branches. Synoptic classification is a means to an end; it is an aid to visualizing growth layers in three dimensions. In the matter of marginal definition, transitions occur in all directions. Apparently no difference exists outward or inward on a branch as regards the incidence—the beginning or ending—of partial growth layers. The same may be said for the trunk as a whole insofar as our work has gone.

A few examples of longitudinal transitions have been cited previously. Nevertheless, specific examples (tables 5 to 44) are here charted to indicate the nature of growth layers grown under extreme lower forest-border conditions. Only a few out of hundreds are given.

In all the tables that follow, the figures in centimeters measure the distance of the cross sections from the respective growing tips, the farthest inward being sections *a*; the vertical succession of growth layers under any one year of a particular section has no relation to the sequence of growth layers in the annual increment; the sharpest and the best-developed growth layers (i.e., sce's) are placed first; and, to the best of our knowledge, a horizontal direction represents continuity or equivalence of the same growth layer outward on the branch. It is to be remarked that the dates given for annual increments have been established with certainty, and no material is included which could have been made uncertain by artificial freezing. If the branches were cut off the trees during the growing season, cutting dates are noted at the end of the tables.

Nearly all tables of this report would be extremely unwieldy without the use of abbreviations. These are here listed not only for use with the text but also for use with the plates and figures.

Abbreviations descriptive of growth layers

abs	absence.
ce	complete, entire growth layer; contact obscure.
ct	curtain.
d arc	diffuse arc.
dce	diffuse, complete, entire growth layer.
ddw	divided densewood.
dL	diffuse lens.
dlw	divided lightwood.
d $\frac{1}{2}$ L	diffuse half-lens.
dw	densewood.
gl	growth layer.
idw	interrupted densewood.
ilw	interrupted lightwood.
inc	incomplete, entire growth layer.
lw	lightwood.

msce	mostly sharp, complete, entire growth layer.
msL	mostly sharp lens.
(p)	probably.
pr x	primary xylem.
psce	partly sharp, complete, entire growth layer.
psg	postseasonal growth.
psL	partly sharp lens.
s arc	sharp arc.
sce	sharp, complete, entire growth layer.
sL	sharp lens.
s $\frac{1}{2}$ L	sharp half-lens.
str	stringer.
tf	tip flush.

TABLE 5.—*Con T 2-3*

	38 cm.	23 cm.	10 cm.
1939	1 sce 1 d arc	1 sce 1 d arc 1 d $\frac{1}{2}$ L	1 sce 2 d arcs

TABLE 6.—*Con T 2-6*

	20 cm.	10 cm.	6 cm.	5.4 cm.
1942	1 sce 2 idw	1 sce 2 idw (faint)	1 sce (1st 1942) 1 sce (2nd 1942)	1 sce (2nd 1942)

TABLE 7.—*SA 5-1*

	73 cm.	60 cm.	46 cm.	28 cm.	2 cm.
1936	2 sce	1 sce 1 sL	1 sce		
1937	1 sce	1 sce	1 sce		
1938	1 sce	1 sce	1 sce 2 s arcs 1 s $\frac{1}{2}$ L	1 sce	
1939	1 sce	1 sce	1 sce 1 sL	1 sce 1 sL	1 sce

TABLE 8.—*TTAp 2-3*

	45 cm.	38 cm.	15 cm.	8 cm.
1938	1 sce 1 psce	1 sce 1 d $\frac{1}{2}$ L		
1939	1 sce (1st)	1 sce 1 d arc	1 sce 1 dce	1 sce 1 dce
	1 psce 2 dL 1 d $\frac{1}{2}$ L	1 dL 1 d $\frac{1}{2}$ L		
1939	1 sL (2nd)	1 sL	1 sce	1 sce

TABLE 9.—*TTC 2-3*

	67 cm.	40 cm.
1937	3 sce 1 sL 1 d $\frac{1}{2}$ L	2 sce
1938	1 sce 1 sL	1 sce 1 sL
1939	2 sce 2 sL	3 sce 1 sL
1940	inc L's	inc L's
Branch cut off March 25, 1940.		

TABLE 10.—*TTC 5-4*

	87 cm.	47 cm.
1934	1 sce	1 msce
1935	2 sce	1 msce
1936	1 sce 1 sL	1 msce
1937	1 sce 2 sL	1 sce 1 dL
1938	1 sce 1 sL	1 sce 1 sL 2 s arcs
1939	1 sce 1 dL	1 sce 1 sL
1940	1 sce	1 ce
Branch cut off July 17, 1940.		

In *TTC 5-4* (table 10), two points should be noted: First, complexity decreases outward in some years and inward in other years; and second, the annual contacts for three years in sections at 47 cm. are partially diffuse.

TABLE 11.—*TTC 5-5*

	56 cm.	16 cm.
1939	1 sce 1 sL	1 sce
1940	1 sce 2 sL	1 sce 1 dL
Branch cut off August 1, 1940.		

TABLE 12.—*TTC 5-6*

	89 cm.	45 cm.
1938	1 sce 1 psce 1 sL	1 sce 1 dL
1939	1 sce	1 sce 2 psce
1 s arc		

In 1938 of *TTC 5-6* (table 12), the 1 sce becomes more diffuse outward in the branch; the lens is concurrent at 89 cm. In 1939 the growth layers are thicker and more numerous outward.

TABLE 13.—*TTC 5-7*

	74 cm.	41 cm.
1937	2 sce 1 s arc	1 sce 2 psce 1 sL
1938	1 sce	1 sce 1 sL
1939	1 sce 1 ddw	1 sce

TABLE 14.—*TTC 5-8*

	72 cm.	14 cm.
1939	1 sce 2 sL	1 sce 2 psce
1940	1 sce 2 sL psg	1 sce 1 sL psg
Branch cut off September 28, 1940.		

TABLE 15.—TTC 5-9

	69 cm.	34 cm.
1936	2 sce	
1937	1 sce 1 msce	3 sce
1938	1 sce 1 sL	1 sce
1939	1 sce	1 sce
1940		1 sce
	1 s conc. L. psg	2 sL psg-slight hint of immature cells.

Branch cut off November 9, 1940.

Among the six branches, TTC 5-4 to 5-9 (tables 10 to 15), variations are numerous both among different years of the same branch and among different branches for the same year.

TABLE 16.—TTC 5-10

	53 cm.	36 cm.
1936	1 sce	
1937	1 sce 1 msce 1 sL	
1938	1 sce	1 sce-more diffuse outward.
	1 msL 1 s arc	1 psce 1 s $\frac{1}{2}$ L
1939	1 sce 1 sL 1 psL	1 sce 2 sL
1940	1 sce 1 psL 1 dl	1 sce 3 sL

TABLE 17.—TTC 5-12

	56 cm.	37 cm.
1937 (2d)	1 sce	
1938	2 sce 1 sL	1 sce
1939	2 sce 1 sL	2 sce
1940	1 sce 1 sL	1 sce 1 sL
1941	inc	inc

Branch cut off May 24, 1941.

The upper portion of the trunk of TTC 12 contained five sharply bordered growth layers in 1935.

In tree TTC 33 a majority of the intra-annuals become sharper margined inward on the branches.

The display of growth layers in 1941 of TTC 34-2 (table 22) was very probably formed by May 18, 1941, because on that date the branch was killed by artificial freezing.

TABLE 18.—*TTC 12-9*

	<i>Inner</i>	<i>Outer</i>
1932	2 sce 1 dce	
1933	1 sce 2 psce	1 sce 1 psce
1934	2 sce 2 psce 1 sL 1 d arc	2 sce 2 psce
1935	2 sce 1 sL	3 sce
1936	1 sce 1 sL	2 sce 1 arc
1937	2 sce 2 psce 1 dce	2 sce 2 msce 1 psce
1938	2 sce 1 dce	1 sce 2 psce
1939	1 sce	1 sce

TABLE 19.—*TTC 12-10*

	<i>66 cm.</i>	<i>34 cm.</i>
1937	1 sce 1 msce 3 dce	1 sce (last of 1937)
1938	2 sce 1 psce 1 dce	1 sce 1 psce 1 ddw
1939	1 psce	1 psce
1940	inc L's	inc

Branch cut off April 21, 1940.

TABLE 20.—*TTC 33-12*

	<i>48 cm.</i>	<i>37 cm.</i>	<i>26 cm.</i>
1941	1 sce 1 dL	1 sce 1 dL	1 sce 1 psL
1942	2 sce ddw	1 sce 1 psce ddw (?)	1 sce 1 dce ddw (?)

TABLE 21.—*TTC 33-13*

	<i>48 cm.</i>	<i>38 cm.</i>	<i>27 cm.</i>
1940	1 sce 1 sL	1 sce 1 psce 1 psL 1 s arc ddw	2 sce
1941	1 sce ddw (faint)	1 sce	1 sce ddw
1942	1 sce 4 sL	1 sce 3 psce psg	1 sce 1 psce psg

TABLE 22.—*TTC* 34-2

	50 cm.	40 cm.	30 cm.
1938	2 sce 1 msce 1 sL 1 dL	2 sce 1 psce 2 sL 1 dL	1 sce 2 msce 2 sL
1939	1 sce	1 sce 1 sL	1 sce 1 dL
1940	1 sce 1 sL 1 d arc	1 sce 1 psce 1 sL 1 s $\frac{1}{2}$ L	1 sce 1 dL 1 d arc
1941	3 sce 1 dL psg	1 sce 2 sL psg	2 sce 2 sL inc L

TABLE 23.—*TTC* 34-3

	56 cm.	50 cm.	43 cm.	32 cm.
1938	1 sce 1 sL	1 sce	1 sce 1 psce 1 dL	1 sce
1939	1 sce 1 sL	1 sce 1 sL	1 sce 1 sL	1 sce 1 msce
1940	1 sce 1 sL	1 sce 1 sL	1 sce 1 sL	1 sce 1 sL

TABLE 24.—*TTC* 34-8

	44 cm.	30 cm.	20 cm.
1941	1 sce 1 dL	1 sce 1 psL	1 sce ddw

TABLE 25.—*TTC* 35-1

	8 cm.	6 cm.	4 cm.	1 cm.
1942	1 sce 1 s arc psg	1 sce	1 sce	1 L

TABLE 26.—*TTC* 35-3

	19 cm.	15 cm.	10 cm.
1944	2 sce inc	2 sce inc	1 dce inc

Branch cut off July 31, 1944.

TABLE 27.—*TTC 35-7*

	23 cm.	17 cm.	12 cm.
1944	3 sce inc	3 sce inc	3 dce inc

TTC 35-7 (table 27) was cut off July 31, 1944. Growth-layer borders increase in sharpness inward on the branch; the growth layers at 17 cm. are much less sharp than they are at 23 cm.

TABLE 28.—*TTC 36-1*

	60 cm.	47 cm.	35 cm.
1940	2 sce	1 sce 1 psce	1 sce ?
1941	1 sce ddw	1 sce	1 sce
1942	1 sce 1 sL 1 s $\frac{1}{2}$ L 1 d $\frac{1}{2}$ L	1 sce 1 sL 1 s $\frac{1}{2}$ L	1 sce 2 sL 1 s $\frac{1}{2}$ L

At 35 cm. in 1942 of TTC 36-1 (table 28), all lenses were less sharp than inward on the branch.

TABLE 29.—*TTC 36-5*

	72 cm.	52 cm.	38 cm.
1940	2 sce 1 msce	1 sce 1 msce	1 sce
1941	1 sce 1 psce 1 dce	1 sce 1 psce 1 dce	1 sce ddw
1942	1 sce 1 psce	1 sce 1 psce 2 dL	1 sce 1 psce 2 dce

TABLE 30.—*TTC 36-7*

	58 cm.	44 cm.	34 cm.
1940	1 sce 1 sL	2 sce	1 sce
1941	1 sce 1 sL	1 sce 1 sL	1 sce
1942	1 sce 1 psce 1 psL 1 d $\frac{1}{2}$ L	1 sce 2 psce	1 sce 2 psce

TABLE 31.—*TTJ 2-4*

	57 cm.	45 cm.	34 cm.
1939	1 sce 2 dce 1 dL	1 sce	1 sce
1940	2 sce	2 sce	1 sce 1 msce
1941	1 sce 1 s arc	1 sce 1 dL	1 sce 1 sL

In the 1940 increment of *TTJ 2-4* (table 31), the outer growth layer comprises one-third on the long radius and one-tenth or less on the short radius of the entire increment. The lightwood of the outer growth layer, at several spots on the short radius, disappears so that the densewood of the inner growth layer lies flush against the densewood of the outer growth layer. This suggests that the transition from a complete growth layer to a lens occurs in two steps: first, the disappearance of the lightwood; and second, the disappearance of the densewood. Transitions of this type apply longitudinally as well as around the circuit of a single cross section.

TABLE 32.—*TTJ 2-5*

	48 cm.	36 cm.	25 cm.
1940	2 sce	2 sce	1 sce 1 dce
1941	1 sce 1 dL	1 sce	1 sce

In the 1940 increment of *TTJ 2-5* (table 32), the outer growth layer has but a fraction of the thickness of the inner growth layer; it is a so-called "outer thin" growth layer whose "thinness" and weakly developed densewood nearly belies the fact that it is the outward termination of an annual increment. The contact of the outer growth layer weakens outward on the branch. The contact of the inner growth layer is sharp at 48 cm., somewhat indefinite at 36 cm., and practically invisible at 25 cm.

TABLE 33.—*TTJ 2-11*

	50 cm.	37 cm.	26 cm.
1940	1 sce 1 sL	1 sce 1 sL	1 sce 1 sL
1941	1 sce	1 sce	1 sce
1942	1 sce 1 psL	1 sce 1 psL	1 sce 1 psL

In the 1940 increment of TTJ 2-11 (table 33), the lens as seen in cross section is a concurrent series of two at 50 cm.; a very long single at 37 cm.; and a shorter single at 26 cm. The lens of 1942 becomes progressively less sharp outward.

TABLE 34.—TTP 20-2

	44 cm.	24 cm.	12 cm.
1938 ...	1 sce 1 dce	2 dce	dw
1939 ...	1 sce 1 dL	1 sce 1 psce	1 sce 1 dce (?)

TABLE 35.—TTP 20-4

	34 cm.	19 cm.
1937	1 msce (1st)	1 dce ddw
1937	1 msce (2d)	1 sce 1 dce
1938	1 msce 2 sL	1 msce

TABLE 36.—TTP 20-16

	18 cm.	14 cm.	9 cm.	3 cm.
1943	1 sce 1 sL	1 sce 1 dL	1 sce 1 dL	
1944	1 sce 1 sL 1 dL	1 sce 1 psL	1 sce 1 dL	1 sce

Nine cm. from the tip of the branch in the specimen TTP 20-16 (table 36), the diffuse lens of 1943 has all but disappeared.

TABLE 37.—TTP 20-26

	3.1 cm.	0.7 cm.
1944	2 sce	1 sce

In TTP 20-26 (table 37), the one growth layer undoubtedly disappears because it ends outward, which is to say that two diameter flushes represent one tip flush.

TABLE 38.—TTP 20-33

	11 cm.	6.5 cm.	2.7 cm.
1943 ...	1 sce 1 dce	1 sce 1 d arc	
1944 ...	1 sce ddw	1 sce ddw	1 sce 1 d arc

TABLE 39.—TTP 21-9

	35 cm.	23 cm.
1938	1 sce	1 msce
1940	1 msce 1 psce ddw	1 sce 1 psce ddw

It is not uncommon to find annual contacts diffusing outward. In 1940 of TTP 21-9 (table 39), as in many other branches, the annual contacts become diffuse inward on the branch.

TABLE 40.—*TTP 24-8*

	51 cm.	40 cm.	34 cm.
1945	1 sce 1 sL	1 sce 1 sL	1 sce

In *TTP 24-8* (table 40), the lens extends out along the branch to 40 cm. but does not exist on the branch as far out as 2.6 cm. from the tip.

TABLE 41.—*TTP 24-14*

	55 cm.	43 cm.	32 cm.
1940	1 sce 1 psce 1 dce	1 sce 2 dce	1 sce 2 dce
1941	1 sce 1 sL	1 sce	1 sce
1942	1 sce ddw psg	1 sce 1 sL ddw psg	1 sce ddw

In the 1940 increment of *TTP 24-14* (table 41), the psce growth layer appears as a lens under very low power because its lightwood disappears over a portion of the circuit.

TABLE 42.—*XSC 1-1*

	81 cm.	68 cm.
1932	2 sce 1 psce	1 sce
1933	1 sce 1 sL	2 sce 1 psL
1934	1 sce	2 sce 1 psL
1935	4 sce 1 psL 1 s $\frac{1}{2}$ L	2 sce 1 dce (outer)
1936	1 msce 1 psce	3 dce
1937	2 sce 2 $\frac{1}{2}$ L	2 dce 1 psce (outer)

TABLE 42.—*Continued*

	81 cm.	68 cm.
1938	1 sce 1 psL	1 sce 1 sL (inner) 1 sL (overlapping) 1 dL
1939	1 sce 1 sL (part compound) 3 psL 1 dL (part compound)	1 sce 1 sL 1 msL 1 s $\frac{1}{2}$ L 1 d $\frac{1}{2}$ L
1940	1 sce ddw inc	1 sce 3 sL 1 s $\frac{1}{2}$ L inc

Branch cut off May 10, 1940.

TABLE 43.—XSC 10-2

	51 cm.	44 cm.	38 cm.	28 cm.
1939	1 sce 1 psce 1 psL	1 sce 1 dce 1 psL	1 sce 1 dce 1 psL	1 sce 1 dce
1940	1 sce 1 dce 1 sL 1 psL	1 sce 1 psce 1 sL 1 psL	1 sce 1 psce 1 sL 1 psL	1 sce 1 msL

TABLE 44.—YCi 1-3

	14 cm.	6 cm.
1940	4 sce	3 sce 1 sL

Tables 5 to 44 give some idea of longitudinal transitions in growth layers. Practically all branch or stem analyses illustrate such transitions. However, attention should also be directed to the following tables: 74 (1944); 81 (1944); 84 (1944); 85 (1938-40); 94 (1940-42); 96 (1940); 105 (1938); 108 (1936-37); 109 (1936-38); 115 (1939); 122 (1939); 126 (1938); and 129 (1938).

An examination of the tables brings out rather clearly that transition from one type of growth layer to another is not a rare phenomenon. Simplicity of growth-layer pattern within the annual increment may increase either outward or inward on the branch, and the same, of course, holds for an increase of complexity. Or again, simplicity

(or complexity) may increase in both directions from a focal point. The evidence also indicates that different species act very much alike and that different branches of the same tree possess different sequences for the same year.

Thus there can be little doubt that growth layers pass from one type to another longitudinally; that the results of one episode of cambial activity may be traced along a branch with more or less difficulty; and that text figures 34 and 35 give a first hint of the variations to be expected among partial growth layers and the reasons therefore.

SUMMARY OF TYPES

In the synoptic view, growth layers group themselves into a relatively small number of distinct types. The simplest classification, whether justified or not, depends upon densewood alone. For instance, a half-lens is a band of densewood dangling at one end. Such is no doubt all right if mere identification is the ultimate aim. It goes without saying, however, that of far greater import is the physiological activity of the cambium which gives rise to the various types of growth layers, types that under a too simple classification would be entirely overlooked. Physiological activity is, in a manner of speaking, a functional bridge between variations in the complex of habitat factors and the type, continuity, and definition of resultant xylem. As an example, the invisible radial termination of a growth layer which extends between the two "open" ends of half-lenses facing each other is quite understandable in relation to physiological activity but is meaningless under a simple classification.

Nevertheless, a descriptive classification in two dimensions is a method of approach to the understanding of growth layers in three dimensions, and their transitions from one to the other. The two-dimensional picture, therefore, takes our attention at the moment.

A condensed outline of growth-layer types follows:

- | | |
|----------------------------|-------------------------------|
| I. Entire | II. Partial— <i>Continued</i> |
| 1. Complete and incomplete | 2. Half-lenses |
| 2. Annual and intra-annual | Simple |
| II. Partial | Compound |
| 1. Lenses | Apposed |
| Simple | Overlapping |
| Compound | Interior |
| Concurrent | Exterior |
| Overlapping | 3. Temporary lenses |
| Interior | 4. Arcs |
| Exterior | Simple |
| Abnormal (densewood | Compound |
| only; low-power lens) | 5. Divided densewood |

II. Partial—*Continued*

6. Divided lightwood
7. Interrupted densewood
8. Interrupted lightwood
9. Curtains
 - Entire
 - Partial

II. Partial—*Continued*

10. Postseasonal growth
 - Scattered cells
 - Lens
 - Concurrent lenses
 - Incomplete, entire growth layer

Factors adding complexities to the above outline will be considered next.

TYPE RELATIONSHIPS

Two points should be mentioned relative to the extension of the simple classification portrayed above. One has to do with so-called invisible margins and the other with the form of growth layers in three dimensions.

The first point considers half-lenses and arcs as actually forming the visible part of closed systems. In the case of apposed half-lenses, the densewood, midway between the cusps, fails, lightwood appears to be continuous radially, and the densewoods of the half-lenses appear to "dangle" or "float" free in the lightwood. In the case of a single half-lens, densewood exists at one cusp only, whereas none is visible either at the median portion of the growth layer or at the apposed cusp. Half-lenses, therefore, represent lenses whose densewood is present only at one or both of the cusps. Hypothetically, densewood may fail at both cusps as well as in the median region. From this we can tentatively conclude that cambial activity and growth processes are cyclic and intermittent whether or not the evidence is anatomically visible; this corroborates similar conclusions by plant physiologists.

Further evidence in the same matter is yielded by divided densewood of certain types, interrupted densewood, and interrupted lightwood.

Arcs may be thought of as belonging to one of three types: (1) A portion of a lens, (2) a portion of an entire growth layer, or (3) possibly an entity whose densewood "floats" free around the entire margin. (1) Here the arc simply is the median portion of a lens or of two apposed half-lenses. This, then, constitutes the complement of the half-lens, that is, the visible median portion compared with the visible cusped portions. (2) In the second type, the arc is the only portion of the densewood present—at least visibly so—around the entire circuit. Thus the arc reveals an episode of cambial activity otherwise unsuspected. The longer the arc is, the more plausible the revelation becomes. (3) In cross section, arcs certainly are entities. But can they retain their characteristics in three dimensions? This leads directly to our next topic.

Point two of the introductory paragraph has to do with the form of growth layers in three dimensions. Entire growth layers may become partial, and vice versa. All various forms of partial growth layers merge the one into the other. *Lenses* may be discrete bodies, like a "patch" on the cylinder of a branch or stem. Or, again, a lens may be the longitudinal extension of a growth layer (text figs. 34, 35). A cross section at one place shows the growth layer to be entire; at another, it appears as a concurrent lens; at a third place, it appears as a single lens; and last, if the section be taken at exactly the correct place, it appears as divided densewood. From a three-dimensional standpoint, lenses testify to cambial activity local in time and space.

Half-lenses represent the visible portions of lenses and as such partake of all variations characteristic of them. Theoretically perhaps, a half-lens could exist independent of a lens, its densewood, sharp for a distance, weakening, diffusing, and giving way tangentially to light-wood. The concept of an independent half-lens is difficult to visualize through physiological activity. In three dimensions, local failure of densewood to form in connection with a lens may produce a half-lens.

Arcs physiologically involve the failure of densewood to form on opposite edges of a lens or lens "finger," or the failure locally of the densewood of an entire growth layer which in cross section gives a long arc. Whether or not an arc can exist independently merits the same remarks as those given in connection with half-lenses.

No matter how we employ cross sections to illustrate growth layers, the three-dimensional aspect cannot be neglected. To do so, is to miss the significance of cambial activity, the important link between growth factors and the anatomy of the xylem.

ECOLOGIC SIGNIFICANCE

The importance of cambial activity has been constantly emphasized both directly and indirectly. Description, classification, and attempted interpretation of growth layers are tasks superficial and misleading without a proper understanding of the physiology of growth. To such a restricted approach, a strictly two-dimensional habit of thought only adds confusion. Growth layers mirror cambial activity and growth processes, and without a knowledge of such activities no solid basis exists for the study of growth layers as a record of the nature and variations of growth factors.

All the work, of which the present paper is a partial report, demonstrates clearly that cambial activity and growth processes within the body of a tree grown under decided lower forest-border conditions are intermittent in time and space both locally and regionally. If

growth factors have any influence at all on the physiological processes, then those processes must respond in nature and, to a certain degree, to the fluctuations of the factors as they exist in the lower forest border. To expect otherwise, is to assume that no factor becomes limiting after growth has begun in the spring until growth stops finally at the end of the growing season.

Classification in its simplest form permits the descriptive designation of growth layers in two dimensions, on cross section or on longitudinal section. In its less simple form, classification emphasizes in three dimensions the rather complex nature of differential cambial activity. Three situations will be summarized.

(1) All types and classes of growth layers appear to merge into each other in three dimensions. This elementary circumstance cannot be too strongly emphasized. Longitudinally, either inward or outward on a branch, divided densewood may become a lens and the lens may become an entire growth layer. An arc may become an entire growth layer. A half-lens may become a lens. A lens may be a "patch" of xylem; or a concurrent lens on a certain cross section may be the "fingers" of an entire growth layer on a different cross section (text figs. 34, 35). Such transitions take place within rather short distances. Therefore, on the basis of one or several cross sections it is unwise to state that a growth layer exists as a lens covering but a tiny percentage of the possible area of the plant body. Growth layers, also, possess all manner of transition between lightwood and densewood, both tangentially and longitudinally. The outer margin of a diameter flush, whether entire growth layer, lens, half-lens, or arc, may grade from sharp through definite, indefinite, to diffuse, and this last may become so diffuse as to be indistinguishable from lightwood. In truth, these gradations apply to all manner of growth layers, entire, partial, annual, or intra-annual.

(2) The above transitions may be thought of as applying to the grosser forms of growth layers—to the more obvious results of intermittent cambial activity. Beyond these, but of course joined to them by transitional forms, there are the indications of slight, more or less incipient, changes in cambial activity and growth processes. Here belong interrupted densewood, interrupted lightwood, and even some cases of divided densewood. A single tangential row of narrow cells (at places so dense as to merit the term "stringer") may be immersed in lightwood, or immersed in other but less decided densewood. On occasion these rows are repeated rhythmically. The conclusion seems warranted that cambial activity and growth processes under lower forest-border conditions do not remain constant in rate over long in-

tervals during any one growing season. Those activities appear to possess not only fluctuations of high amplitude and long wavelength, giving the ordinary growth layers, but also fluctuations of slight amplitude and short wavelength, giving what may be called crypto-growth layers. The short-wave cycle is no doubt superimposed upon the long-wave cycle.

(3) The third situation has to do especially with transitions in a radial direction. Typically, a growth layer is thought of as being complete if the ratio of lightwood to densewood is rather high in favor of the lightwood. A decrease in width of one commonly accompanies a decrease in the other so that if the lightwood consists of few cells radially, say three or four, the densewood may be reduced to one cell only. Nevertheless, the typical situation has striking exceptions, the one radial, the other tangential, insofar as the lightwood is concerned. It may be reduced in amount radially until the densewood comprises a very high percentage of the total growth layer. Or, the lightwood may be reduced tangentially until it disappears entirely and the densewood of that growth layer then lies sheer against the densewood of the next inner growth layer. This results in a lens of lightwood which under low magnification appears to be a complete and bona fide lens. Such an error in recognition would lead to an entirely erroneous interpretation of the regional extent of cambial activity and of the amount of xylem formed during the particular growth flush.

Certain particulars of the subject in hand should be mentioned in more detail. The amounts and proportions of lightwood and densewood, for instance, vary radially and longitudinally in absolute and relative fashion. Apparently the densewood varies to a much greater extent than does the lightwood. In the loblolly pine, Con T 2-o-base a, the densewood of 1943 varies in thickness, whereas the lightwood remains constant around the circuit. Arizona cypress is prone to great variations. In TTC 36-7-a, for instance, the densewood of 1938 ranges from a thick band constituting a high percentage of the complete growth layer to a very thin, weak band constituting a slight percentage of it. These variations may exist in one growth layer on one section, or they may be on different branches. On a single section, the densewood may be but one cell thick on one radius and may increase in thickness tangentially to many cells far exceeding the lightwood. A growth layer toward the extreme may contain only one lightwood and one densewood cell, or the lightwood cell may fail, leaving a growth layer represented by one row of densewood cells.

The maple, TTM 1, gives a very slight hint that there may be a relationship between amount of tip growth and amount of lignification,

at least as far back as 32 cm. from the tip. In TTM 1-1 and 1-2, where tip growth was extensive, only slight lignification took place in the xylem either in densewood or lightwood. In TTM 1-3, in contrast, where tip growth was rather slight, lignification of the xylem was much more pronounced, especially in the densewood.

The 1941 increment in TTC 34-2-c (table 22) contained 2 sce plus 2 sL plus 1 inc L. All these were formed prior to May 18 because on that date the cambium was killed by artificial freezing. In relation to their total thicknesses the growth layers possessed heavy bands of densewood. As a matter of fact, these bands on some radii were even heavier than the densewood of the 1940 increment which was a growth layer six times as wide as any of the 1941 intra-annuals. The case of TTC 34-2-c thus presents the problem as to the possible cause of densewood variation, whether due to variation of climate, food supply, or the part of the season when deposited.

The entire subject of partial growth layers is intimately connected with the place where cambial activity is initiated. Longitudinally there is evidence that diameter growth begins at some point back of the tip and spreads both outward and inward on the branch. It is clear, at least, that growth does not necessarily begin at the tips of the branches and spread uniformly inward and downward. In all likelihood there are multiple foci of growth initiation, something to be expected in the light of growth-layer types and of waves of cambial activity.

Transversely, evidence shows that the cambium becomes active at one or more foci from which the activity spreads. Two variations stand out when sections are cut or killed so as to interrupt growth at successive stages. At the start, new xylem appears as a few isolated single cells around the circuit or as one or more tiny clusters of cells. The isolated cells eventually are joined by others and thus become lenses. All the evidence of the present study strongly suggests that all growth layers begin as lenses. Therefore, partial growth layers are entire growth layers whose development was arrested or prevented before the entire cambium became active.

In the sections of TTC 12-10-a, cut April 21, 1940, growth for 1940 consists radially of one to eight cells and tangentially of one long and one very short lens (table 19). The inner half of the long lens is strongly lignified. In branches which are eccentric, new growth commonly, but not always, appears first on the long radius or on what will be the long radius for that growth flush.

Growth for 1940 in TTC 1-10-a, cut April 21, 1940, covers the entire circuit, 8 to 16 cells thick radially. On the long radius, and covering most of the circuit, the inner three-quarters of the growth layer has matured, whereas on the short radius all cells are immature.

An interesting case of differential growth exists in TTC 5-4-a. Within the densewood of 1933, a circle of parenchyma cells extends around the circuit at a uniform distance from the inner margin of the growth layer. The circle lies just next to the outer contact of the growth layer on the short radius, whereas on the long radius it lies 12 to 15 cells inward from the contact but still within the densewood. Either cambial activity proceeded at a more rapid rate on the long radius after the formation of densewood began or, what may be more likely, activity continued for a greater length of time on the long radius.

High amplitude waves of cambial activity appear to develop rapidly after the start of the growing season, reach a maximum, and subside either intermittently or continuously. Such activity merely reflects the impact of physiological processes. Examples of time and time rate of activity have been cited heretofore. Growth initiation in the spring in the Lubbock area may occur any time from the first part of March to the first part of April. Within a very short period, growth attains a maximum and then gradually subsides, the whole flush occupying roughly anywhere from about 4 to 12 weeks. Apparently no simple relation exists between elapsed time and number of cells laid down. In one case, several growth layers may be deposited, while in a second, a single growth layer is formed. These variations of time rate apply not only among different trees but also among different branches of the same tree.

The following examples may be recalled. The increment for 1941 of TTC 34-2-c whose cambium was killed May 18, 1941, contains 2 sce plus 2 sL plus 1 inc L. The 1940 increment of TTC 12-10-a, cut April 21, 1940, consists of one to eight cells radially, in one long and one very short lens. In TTC 1-10-a (pl. 4, fig. 2), cut April 21, 1940, the same increment consists of 8 to 16 rows of cells around the entire circuit. The same increment in TTC 5-4-a, but cut July 17, 1940, contains 8 to 20 cell rows as an entire growth layer. To say that growth begins on a certain date does not mean that the entire cambium becomes active at the same time. The position of natural frost injury, or a circle of parenchyma cells, is an excellent example (pls. 8; 14, fig. 1). The injury may be out in the xylem 7 to 10 or more cells from the start of the growth layer; it may be out a large number of cells on the long radius but lie flush against the densewood of the previous growth layer on the short radius; or it may be out in the xylem on the long radius, pull inward on both sides of that radius, meet the densewood of the previous growth layer, and cease (pl. 22, fig. 1). Thus in the last case a decided lens had been formed before the cam-

bium on the short radius became active. The extreme variation of cambial activity in a decided lower forest-border situation not only among different trees but among branches of the same tree also comes into relief by contrasting the thick growth layers of 30 or more cells with the situation noted in TTP 24-3-a and kindred sections (pls. 17, fig. 1; 19, fig. 1). There a growth layer, represented elsewhere in radial thickness by many cells, is made up of one densewood cell over a portion of the circuit and by very few more over the remainder.

Cambial activity may be related to the absolute vitality of the cambial initials. This may be illustrated by several branches of TTP 20, a tree probably of less than average vigor.

TABLE 45.—TTP 20-1

	37 cm.	5 cm.
1939	1 sce	1 sce
		1 dL
		psg

Branch was cut off November 26, 1939.

At 37 cm. in TTP 20-1 (table 45), the condition of the cambium was variable; some cells were alive, some plasmolyzed, the rest dead. At 5 cm. most of the cambium was alive.

TABLE 46.—TTP 20-2

	44 cm.	24 cm.	12 cm.	Bud
1939	1 sce	1 sce	1 sce	1 inc
	1 dL	1 psce	1 ce (faint)	(narrow cells in patches)

Branch was cut off December 14, 1939.

The outer cells of the xylem in TTP 20-2 (table 46) were immature. At 44 cm. cambial cells were in part nucleated, in part plasmolyzed; at 24 cm. the cambium was in good condition; at 12 cm. and at the bud it was excellent.

TABLE 47.—TTP 20-3

	18 cm.	11 cm.	Bud
1939	1 concurrent L	1 conc. L	1 psce (part immature)

Branch was cut off December 15, 1939.

At 18 cm. in TTP 20-3 (table 47), the cambium was mostly alive, some cells plasmolyzed; at 11 cm. and at the bud the cambium was in good condition.

TABLE 48.—*TTP 20-4*

	34 cm.	19 cm.
1939	1 long ps p inc L	1 ps p inc 1 dL

Branch was cut off March 25, 1940.

At 34 cm. in *TTP 20-4* (table 48), the cambium had a few good cells and many completely plasmolyzed. Outer xylem cells were partly immature; densewood was poorly developed at places. At 19 cm. the cambium had a few good cells and many plasmolyzed cells. Outer xylem cells were partly immature; densewood graded from normal to weakly developed to absent.

The increment for 1939 in *TTP 20-5*, cut February 29, 1940, consists of a short, very thin lens on the short radius whose outer margin varies from sharp to diffuse. Actually, the densewood is so poorly developed that, if the section were to have been cut several years later, 1939 would have been a diffuse lens were it identifiable at all. The cells of the cambium are for the most part empty or plasmolyzed around the entire circuit, the exception being the cells immediately over the 1939 growth layer. As a summary of *TTP 20-1*, 2, 3, 4, and 5: the cambium was in better condition in those sections where the growth layer is entire; and where it is a lens, the cambium was in better condition over the lens than elsewhere. The first conclusion to come to mind is that there is an explanation of lenses—dead cambium. Such, however, would entail a great many complex physiological processes in the repeated local death and regeneration of the cambium, necessitated by many of the sections hitherto used as illustrations.

No attempt will be made here to explain reaction or compression wood. So far as classification and multiplicity are concerned, the effects of compression wood were taken into consideration or else the sections were not used. Compression wood seems to be a much more sensitive recorder of small-amplitude fluctuations in cambial activity than ordinary xylem. In many instances the presence of the abnormal cells at the start of a growth layer masked the nature of the contact unless high power was used. Instances exist where the complete growth layer was composed of compression wood except for the outer two or three rows of cells which were normal.

DEFINITION OF A GROWTH LAYER

A consideration of growth-layer types, of their intergradations in three dimensions, and of their relationships to physiological processes reveals that it is no simple matter to define a growth layer. The defini-

tion that a growth layer is a sheath of xylem laid down under the bark over the entire plant body (except in stem tips and root tips) refers to one type of growth layer only. Or, the definition that a growth layer (or tree ring) is a circle of wood made up of springwood and summerwood refers only to appearances on a cross section.

It seems reasonable to ask for a definition based not only upon description or structural features but also upon those physiological processes which create the growth layer. Thus a certain type of physiological activity may be called a growth flush if it produces a growth layer. *A growth flush is an interval of physiological activity* which gives elongation at the apical meristem and increase in diameter at the cambium. This does not mean to deny the possibility of a period of accelerated physiological activity without the production of wood or the possibility of including the processes of maturation as part or all of a growth flush. On the whole, a growth flush may be slight in intensity and short in duration, or severe and prolonged.

A growth flush commonly produces a growth layer. More specifically, a growth layer includes the xylem laid down by the cambium during a single period of activity regardless of entirety around the circuit, of completeness radially, of location within the plant body, or of the particular time of the activity.

VI. MULTIPLICITY OF GROWTH LAYERS

INCIDENCE OF THE SINGLE ANNUAL

Previous discussion contains many references to multiplicity—multiplicity within annual increments from trees grown at the lower forest border. By means of absolute dating the existence of such multiplicity is established. Also the use of absolute dating permits the collection of statistical data on the ratio of single to multiple annual increments.

Table 49 contains information on dated growth layers. Con T may be used as an illustration. Within 41 branches (from 3 trees) there are 49 years with a single growth layer per annual increment in all sections of the particular branches for the particular years; there are 7 years with both single and multiple growth layers along the same branch; and 44 years with multiple growth layers per annual increment in all sections of the particular branches for the particular years.

The chief concern here is the relative incidence of single and multiple growth layers in the total picture. With 336 years bearing single growth layers and 583 bearing multiples, the respective percentages are 37 single and 63 multiple. The value of 63 percent is a minimum because in 158 years some of the annual increments have multiple

TABLE 49.—*Incidence of single and multiple growth layers in annual increments*

	Number of trees	Number of branches	Number of blocks sectioned	All single	Single and multiple	All multiple
CCCb	1	1	1	—	—	5
CMJ	1	1	2	—	—	4
Con A	1	1	2	—	—	2
Con P	1	2	4	1	—	3
Con T	3	41	148	49	7	44
MP	1	2	7	—	1	2
SA	2	6	16	15	3	14
TTAp	2	7	27	—	4	10
TTC	10	86	225	47	54	143
TTCw	1	7	14	7	2	2
TTJ	5	21	59	30	12	28
TTL	5	15	27	25	—	2
TTM	2	12	35	9	5	7
TTP	5	97	260	112	43	97
TTS	1	1	1	1	—	4
TTTh	1	1	1	1	—	3
TTV	1	1	1	—	—	3
WAp	1	2	7	1	—	2
WCh	2	6	14	—	6	2
WPe	1	6	19	2	2	3
WPl	1	2	5	2	—	—
XSC	11	40	118	19	15	157
XSJf	2	3	7	6	—	7
XSP	2	5	10	9	3	11
YCt	4	14	26	—	1	28
Total	67	380	1036	336	158	583

growth layers whereas others have single growth layers. Therefore, the actual percentage of years with multiple growth layers is somewhat greater than 63. It must be remembered, of course, that some of the years with singles may actually have been multiple at places on the branches not represented by sections.

Among the trees from which many sections were cut, species does not seem to be the controlling factor in multiplicity. The following show more than 50 percent of the years with multiple growth layers: loblolly pine (Con T), shrubalthea (SA), apple (TTAp), Arizona cypress (TTC), juniper (TTJ), cut-leaf or soft maple (TTM), yellow pines (TTP), cherry (WCh), peach (WPe), Arizona cypress (XSC), ponderosa pine (XSP), and citrus (YCt). In contrast, the cottonwood (TTCw), the honeylocust (TTL), and the Jeffrey pine (XSJf) show less than 50 percent of the years with multiple growth layers.

It should be emphasized that two to four cross sections only are taken roughly equal distances apart out of a 50-cm. length of branch. Perhaps this number could be considered too few to serve as random samples, yet partial growth layers do have a longitudinal dimension thus permitting each cross section to represent more of the branch length than just its own thickness. This probability of two to four sections revealing all cases of multiple growth layers applies naturally to those cases where multiplicity is caused by partial growth layers only.

In view of the mass of evidence accumulated in our cross sections and in view of the nature of growth conditions in the lower forest-border regions, it may well be that few, very few, annual increments throughout their extent over roots, trunks, and branches possess only one growth layer. Growth factors first, and species second, seem to be of importance in determining the incidence of multiple growth layers in annual increments.

It is of interest to note that 1,036 out of a total of 1,245 sectioned blocks taken from branches and trunks were dated accurately. The remainder were obtained almost wholly from New Mexico on field trips so brief that the growth layers could not be dated by our methods.

STATEMENT OF THE PROBLEM

Here we are dealing with normal growth layers in normal trees; that is to say, those not subjected to the sudden, or prolonged, impact of such accidental factors as fire, wind, disease, defoliation, or insect attacks.

Discussion has cropped up intermittently through the years on the unity or multiplicity of growth layers in annual increments. In many cases, certainly, both aspects of the problem are correct, the response of the trees being dependent upon the particular set of growth factors present. That a tree forms one and only one sharply bounded growth layer a year, or that a tree can form more than one a year—either of these is an assumption unless supported by adequate evidence.

Certain implications follow from the idea of rigid unity. First, it implies that growth begins in the spring and goes to completion, a completion signaled by a sharply defined outer surface everywhere throughout the extent of the growth layer. Second, it implies that growth, especially cambial activity, cannot be reinitiated during the same general growing season after growth has once completely ceased. This must be true no matter how brief or how prolonged the original growth flush might be at the beginning of the season. Third,

it implies a special set of growth-initiating factors that impinge successfully on the physiological system of the plant only at the start of the season and, once having been counteracted, cannot stimulate that system into growth again until the opening of the next season. Fourth, it implies that growth can slow down to any degree short of a condition producing a sharp outer surface. If a sharp surface is produced it at once becomes the outer surface of an annual increment. Fifth, it implies that, as a result of the fourth implication, all so-called doubles are diffuse, never sharp. Sixth, the maximum number of sharply bounded growth layers in a tree reveals the true number of years involved. Finding the age of a tree, or dating specific events, rests, therefore, upon the exact determination of the maximum number of sharply bounded growth layers within the entire plant body, roots, trunk, and branches. The entire plant body is included of necessity because in and near the lower forest-border partial growth layers are characteristic and enclose variable areas on the plant body.

Implications inherent in the idea of multiplicity contrast vividly with those embodied in unity. First, it implies that growth not only can slow down and cease completely *within* a single season but also can begin anew. Second, the combination of growth factors present at growth initiation in the spring can also be present later during the general growing season. Third, it implies that growth having ceased so completely as to form a sharply bordered growth layer can begin again during the same season. Fourth, it implies that fluctuations in cambial activity and growth processes accompany fluctuations in growth factors. Such activity can be slowed down to various degrees or cease altogether and even though it cease completely, can be reinitiated the same season. Fifth, it implies that multiplicity and unity are characteristics dependent to a great extent upon environmental conditions. Sixth, it implies that the maximum number of sharply bordered growth layers does not represent the true number of years involved—it exaggerates that number. Counting the sharply bordered growth layers, therefore, does not determine the age of a tree and does not date specific events unless the tree grew under conditions where growth factors do not fluctuate in critical amount except once per year and where, therefore, unity is the rule.

Unity and multiplicity reflect cambial activity, activity which responds to conditions favoring or inhibiting growth.

If multiplicity exists and if it depends upon environmental conditions, it must occur to different degrees. To state the matter from the standpoint of the trees themselves: the ratio of multiple annual increments to single annual increments must vary from region to region

as environment differs. This ratio, or the incidence of multiplicity per century, can be determined for different regions.

Multiplicity, as exemplified by partial growth layers, may or may not characterize different parts of the plant body. If partial growth layers should, for instance, characterize branches but avoid the trunk, then we can only conclude that branches give more sensitive records of environmental variations than trunks do. This matter of longitudinal continuity has been, and is being, investigated. As far as our work has progressed (chapter VII), the anatomy of growth layers and their multiplicity are very similar in branch and in trunk.

TYPES OF GROWTH LAYERS INVOLVED

Multiplicity involves all types of growth layers as well as all types of contacts. The section on classification describes growth layers

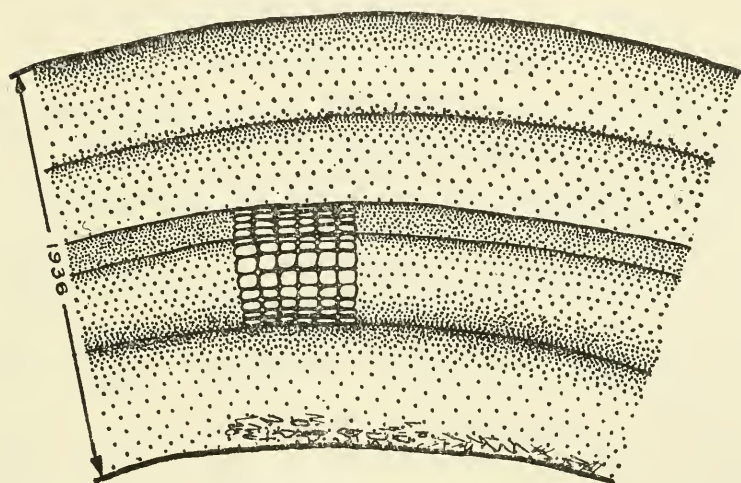


FIG. 36.—XSC 2-2-a. Annual increment for 1936 in symbol and cell structure. Multiplicity by sharp and diffuse gls; reversed sequence. Sequence shows: Frost effects; dce with transition outward giving lightest wood in center; 2 sce; psce; sce.

which range from divided densewood and “stringers,” through arcs, half-lenses, and lenses, to entire growth layers, and from incomplete and subnormally developed to complete, normal growth layers. In the matter of contacts the range is equally great, from sharp through definite and indefinite to diffuse (text fig. 36). Each type of contact may apply to a whole growth layer, or all types may exist on the same growth layer.

Thus the growth layers found in branches may be said to arrange themselves in a series from completely diffuse and local to completely sharp and regional within the tree. All types of growth layers and all types of contacts exist among growth layers, whether annual or intra-annual.

ABSOLUTE DATING AND THE DETECTION OF MULTIPLICITY

The whole range of growth-layer types is highly suggestive of multiplicity. Indeed, a close study of the gradual and complete transition from interrupted lightwood, interrupted densewood, divided densewood, and divided lightwood through the whole gamut of partial growth layers to complete, entire growth layers convinces the student that he is dealing with intra-annuals as well as with annuals. To think that a tiny lens, one or two cells in thickness and a fraction of one percent of the stem in area, can represent the total growth of a normal tree for a period of one year becomes increasingly impossible as a person studies cambial activity. The same feeling based on intimate acquaintance with trees comes in regard to partial growth layers or even entire growth layers if they contrast strikingly in volume with the average growth layer of the tree. Perhaps that is why Antevs (1938) was a bit skeptical of the annual character of a thin ring whose volume contrasted sharply with that of neighboring rings.

It may not be amiss to mention another facet of the subject based upon general impressions and observations. Scarcely a region exists which does not, for that region, experience temporary droughts during the growing seasons. Vegetation responds not only to such temporary droughts but also to warm, wet intervals. It responds visibly; for instance, beech trees shedding their leaves in central Ohio during a midsummer drought; the madroña dropping its leaves habitually during the summer along the coastal region of California; the withering of crops; the curling, drying, or dropping of leaves from fruit and nut trees in Maryland; the ocotillo putting forth a new set of leaves after each summer rainy period; the blossoming of fruit trees late in the summer in Maryland and Washington, D.C.; the setting of fruit and substantial tip growth in late summer in West Virginia; the blossoming of fruit trees and spring flowers in early September in Minnesota; the swelling of buds and tip growth in Texas, not only in the autumn but also during the winter; the addition of complete tip flushes on pines high in the Sierra of California in late summer; and the addition of complete tip flushes after each irrigation of citrus in Arizona. These observations give a vivid impression of growth flushes dependent upon the fluctuation of growth factors

within the general growing season, flushes imposed upon the annual cycle. Adding together the fact of postseasonal growth and the addition of an entire growth layer by irrigation of an apple tree in Texas, one becomes firmly convinced that anatomical results are certain to follow if growth factors become sufficiently limiting for a short interval during the "growing season."

Nevertheless, general observations must be substantiated by actual evidence and proof that trees do grow multiple growth layers in a year. Absolute dating is a necessity. For such purpose, these criteria of multiplicity have been employed: natural frost, artificial frost, measured tip growth, certain structural features, and the relation of diameter flushes to tip flushes.

Examples of dated multiplicity are shown on most of the plates. See especially plates 2, fig. 3; 4, fig. 1; 6, fig. 1; 8; 10, fig. 1; 14, fig. 1; 15, fig. 2; 19, fig. 1; 20; 21; 22, fig. 2; 23, fig. 2; 24, fig. 1; 28, fig. 2; 29; 32; 35, fig. 1; 36, fig. 1.

DETAILS OF MULTIPLICITY

The step immediately subsequent to the recognition of the galaxy of partial growth layers follows logically. It is the great and expected diversity among growth-layer sequences, on different radii of the same cross section, at different levels in the same branch, in different branches of the same tree, in different trees of the same species, among different species, and under different environments.

Clearly, a knowledge of the exact, and not the assumed, date of each growth layer is of the highest importance to a problem of this kind. Assumptions about one, or more than one, sharply bounded growth layer per year must be eliminated. The idea of a rigidly annual unity of growth layers universal in occurrence would be destroyed as such, once multiplicity is established. That done, the fact of unity or multiplicity must be determined for different environments and, where multiple, the incidence or factor of such multiplicity must also be determined.

How can interpretations based on unity be valid if not unity but multiplicity is present in a region? There can be no doubt that chronologic, climatic, and cycle studies are meaningless until fundamental work on growth layers has been done and the effects of different environments clarified.

VARIATIONS OF SEQUENCES ALONG DIFFERENT RADII OF A SECTION

The existence of partial growth layers constitutes a prime reason for the variation of sequences on different radii of the same cross

section. But partial growth layers are not the only variables—the nature of the outer surface of a growth layer varies from sharp to indefinite, to diffuse, and even to a faintness that makes the surface scarcely identifiable.

The incidence of partial growth layers is directly proportional to the number of intervals of localized cambial activity and maturation, and these intervals depend upon the fluctuations of growth factors or of their stimulating qualities. If soil moisture is of great importance to tree growth, then partial growth layers should no doubt characterize the lower forest border. Further, the more extreme the forest-border conditions are, i.e., the more rapid and more intense the fluctuations of soil moisture, the greater the incidence of partial growth layers. A greater incidence of partial growth layers carries with it more rapid variations among different radii of the same cross section.

Therefore, as rainfall decreases, as amplitude of rainfall variations increases, and as lower forest-border conditions become more extreme on the side of aridity (i.e., plant growth is more and more dependent upon the individual local rain), different radii vary with each other within shorter distances and to a greater degree.

Nearly every example used in this work illustrates some form or characteristic of multiplicity. Even so, a few pertinent cases will be cited to illustrate variation among radii on the single cross section. A comparison of figure 2, plate 5, and figure 1, plate 6, and figure 2, plate 6, and figure 1, plate 7, illustrates the differences which can exist on opposite radii.

Specimen TTC 33-10-a contains dated growth for 1938 to 1942, five years. An over-all analysis of the section gives:

TABLE 50.—TTC 33-10-a

1938—1	sce
1939—2	sce+1 psce+1 sL
1940—1	sce+1 psce
1941—1	sce+1 psce
1942—2	sce+1 sL

Three points should be mentioned. First, with seven sharp, complete, entire growth layers and two sharp lenses and three partly sharp, complete, entire growth layers, different radii must show variable numbers of sharp contacts. Second, four radii, 90 degrees apart, contain 9, 10, 7, and 9 sharply bounded growth layers. How could these be correlated with each other if just the four radii, and not the entire section, were available? Third, if we momentarily adopt the assump-

tion that each sharply bordered growth layer must necessarily be an annual increment, we have the interesting but impossible situation of nine annual increments for five years.

Much the same information is yielded by TTC 36-7-b (text figs. 25, 26) which includes four years, 1939-1942. A general analysis gives:

TABLE 51.—TTC 36-7-b

1939—1 sce+ddw

1940—2 sce

1941—1 sce+1 sL+1 d $\frac{1}{2}$ L

1942—1 sce+1 psce+2 s arcs+1 d arc

Here, four years include six sharp growth layers. Some radii show seven sharp contacts and one radius gives the maximum of eight sharp contacts under low-low power.

Four radii have been selected on TTC 33-6-a (text fig. 5). The differences between radii 2 and 3, and 1 and 3, are especially noteworthy. In fact, the sequence of sharp contacts is different on each radius and one can readily see the difficulties inherent in correlating from one radius to another if the surface of the section between two radii is unavailable. As a matter of passing interest, tip growth of branch TTC 33-6 was measured February 21, 1942, January 9, 1943, January 22, 1944, and July 31, 1944, when the branch was cut off. Sections *a* were cut from the 1942 tip growth. Because this branch was growing when cut, at least one more growth layer would have been formed before the general close of the growing season.

The growth of one year is equally effective as an illustration of radial variation. Text figure 30 of TTC 33-11-a, shows the growth increment of 1940 on two opposite radii. Without the rest of the section, correlation would be neither simple nor certain. The interior of the increment actually contains two simple arcs and one compound arc. It is the central arc which is compound and diffuse at one extremity and sharp bordered at the other. Over more than half the circuit the outer densewood zone is divided into three bands, elsewhere into two, the entire zone being referred to as multiple densewood.

Text figure 37, TTC 33-13-a, shows the increment for 1942 wherein a radius can be so chosen as to contain 1, 2, 3, 4, or 5 sharp contacts.

Although text figure 13, XSC 1-1-b, does not contain the entire cross section, enough of 1939 appears to show that the 1939 annual

increment can be made to yield 1, 2, 3, or 4 sharp contacts depending upon the radius selected.

Text figure 15, XSC 1-1-b, has the increment for 1940 only. If different radii are drawn on the figure, it becomes apparent at once not only that great variation exists but also that correlation among the different radial sequences, were they alone available, would be extremely difficult, if not wholly impossible.

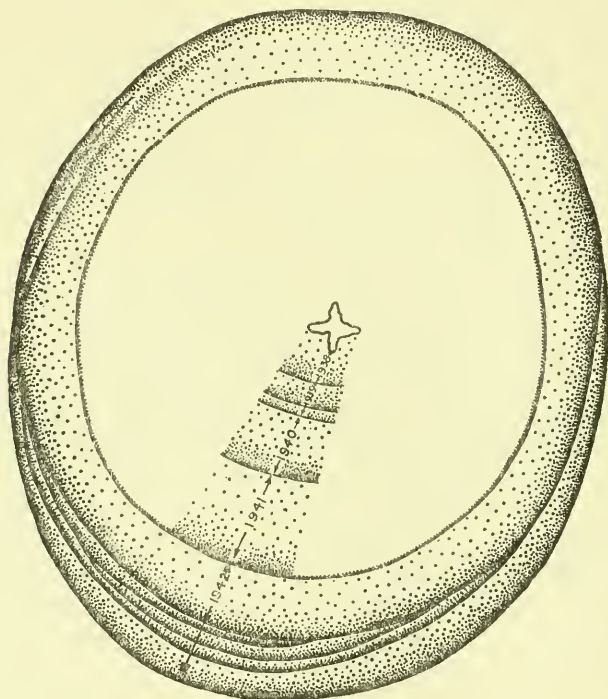


FIG. 37.—TTC 33-13-a. Complete increment for 1942 and a radius extending to the center. 1938: sce (as shown); 1939: 2 sce; 1940: sce; 1941: sce; 1942: sce with 2 $\frac{1}{2}$ L's and 4 sL. Multiplicity; compound and overlapping lenses illustrating variable cambial and growth activities.

Other examples of different radial sequences on the same cross section are: text figures 38 (TTap 2-3-b), 39 (XSC 2-1-b), 40 (XSC 2-2-c), 2 (XSC 8-4-a), 3 (XSC 1-4-a), 10 (XSC 1-2-a), and 22 (XSC 1-3-b).

The section XSC 13-2-a is somewhat of a special case because in the increment for 1938, containing 1 sce + 1 msce + 1 s arc, the sharp portion of the arc lies radially outward from the diffuse part of the msce and overlaps its sharp ends (pl. 33). Thus, by reason of the

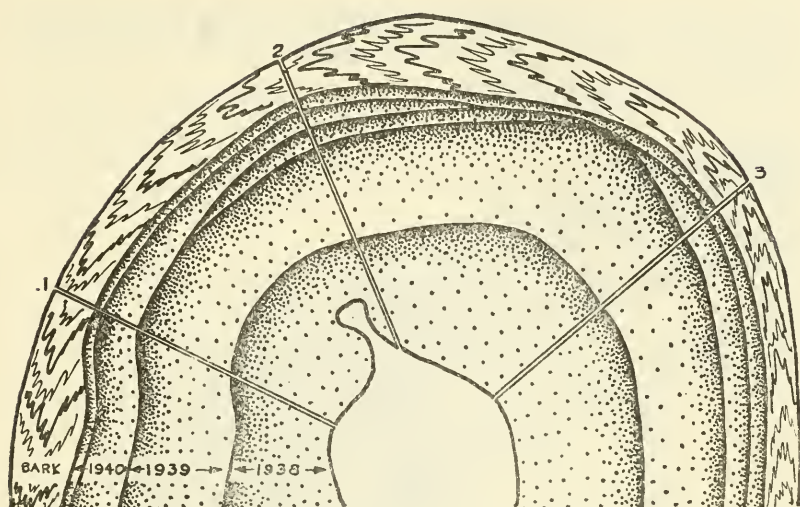


FIG. 38.—*TTA* 2-3-b. Increments for 1938-1940. Different number of contacts along different radii; variation of cambial activity in time and place.

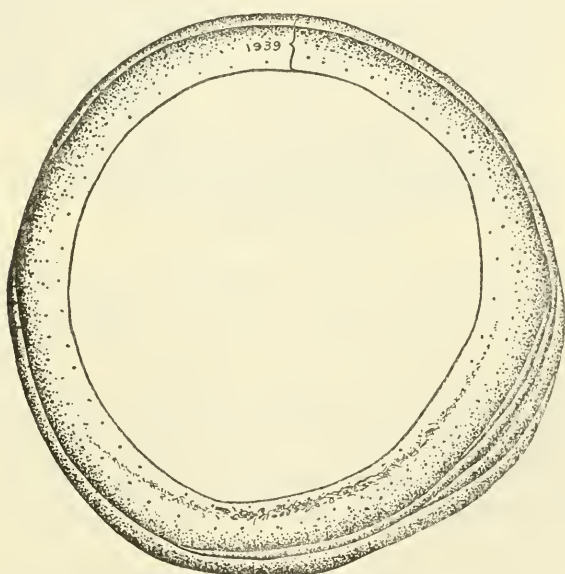


FIG. 39.—*XSC* 2-1-b. The increment for 1939. Multiplicity; partial gls with compound overlapping lenses. Sequence as follows: sce; short sL; long msL, compound with previous sL; short sL, compound with previous 2 lenses; long sL, overlapping previous short sL and long msL. Note that the two outer lenses whose cusps nearly meet are not the product of the same episode of cambial activity.

overlap, there are six sharply bounded growth layers for four years on the entire section, no matter which radius is selected. But they are not all the same growth layers.

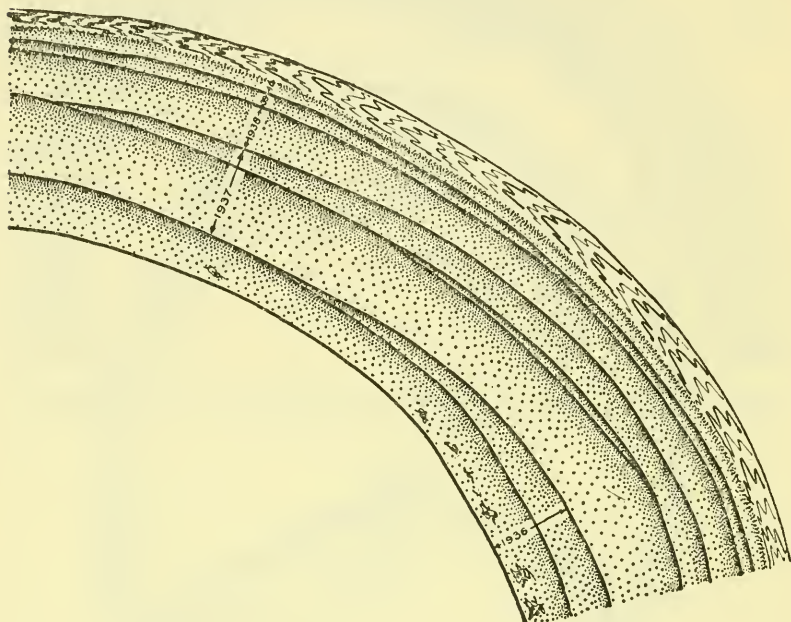


FIG. 40.—XSC 2-2-c. Increments for 1936-1939, and portion of 1940. Part of a section with simple multiplicity. 1936: Spots of natural frost; sce; sL; 1937: sce; compound sL; 1938: sce; 1939: sce; 1940: inc.

Text figure 41, TTC 5-11-a, furnishes an apt summary of radial variation. To be sure, the section seems to be exaggerated because of decided eccentricity. Nevertheless, the numerous intra-annuals, which are but partially responsible for the eccentricity, record the number of times the cambium was stimulated into activity and also the number of times it became inactive. Another point in summary, this section along with many others proves that annual increments can be made up of multiple growth layers whose outer faces are sharply defined.

It is clear, therefore, that a single radius or an increment core from one tree grown under certain environmental conditions would give a rather inadequate record of the total growth of that tree; even several cores taken at one level or a substantial portion of a section would not necessarily represent the remainder of the trunk.

VARIATION OF SEQUENCES ON DIFFERENT SECTIONS OF THE
SAME BRANCH

Variations among sequences along the length of a branch exist for the same reasons that they do among different radii of one cross section. However, they are neither so numerous nor so striking because whole sections are compared rather than single radii. If various radii

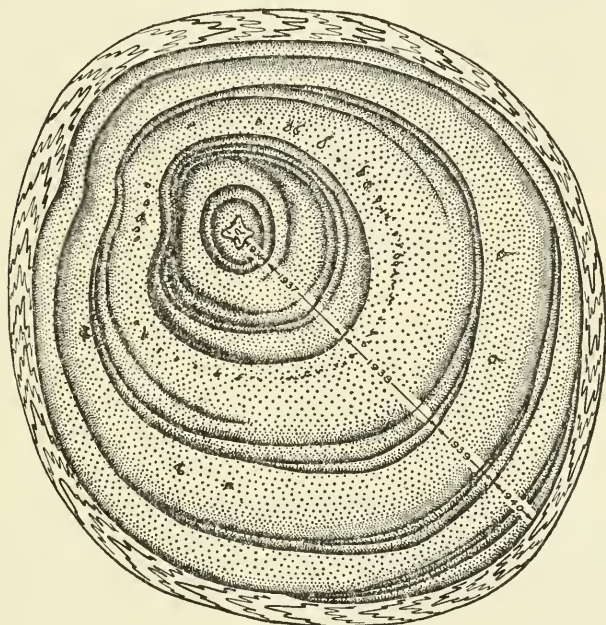


FIG. 41.—*TTC 5-II-a*. Increments for 1936-1940. Multiplicity and complex lensing. 1936: 2 sce; 1937: $\frac{1}{2}$ L's; msce; 2 sce; sL; 1938: natural frost effects; long arc; msce; compound sL; 1939: frost spots; sce; compound sL; 1940: d $\frac{1}{2}$ L; sce; compound sL.

on one section were compared to various radii on the other sections, the differences would be equally numerous and equally striking. This is to be expected because partial growth layers are not only local around the circuit but also local along the length of a branch. In addition, a partial growth layer may be multiple in its existence longitudinally. A lens, for instance, may be concurrent along the branch as well as around the circuit of a cross section.

Examples will be given for the double purpose of illustrating longitudinal variations and the building of a well-rounded picture of growth layers in all their manifold classes. Under the section on longitudinal variations, in the chapter on classification, examples have

already been detailed to some extent. This display may now be extended and amplified. The abbreviations given on page 101 are pertinent to the present detail. Here, also, the figures in centimeters measure the distance of the cross sections from the respective growing tips and, it is to be noted, the dates given have been established with certainty.

In the tables which follow (tables 52-141), the vertical succession of growth layers under any one year of a particular section has no relation to the sequence of growth layers in the annual increment. The sharpest and the best-developed growth layers (i.e., sce's) are invariably placed first. Each individual growth layer, however, is followed outward on the branch by the horizontal direction in the tables. Cutting dates are mentioned where they are of direct importance to the development of the last annual increment.

TABLE 52.—*TTAp 1-4*

	60 cm.	54 cm.	25 cm.	5 cm.	TF
1938	1 sce 2 dce	1 sce			2
1939	1 sce 1 s arc	1 sce 1 s arc	1 sce	1 sce	1
1940	inc	inc	inc	inc	1

Sections were cut from branch *TTAp 1-4* (table 52) April 21, 1940. The growth for 1940 thickens outward on the branch. Two points should be made: First, four tip flushes (TF) at a minimum represent three growing seasons, one of which is incomplete; and second, certain radii at 60 and 54 cm. possess three sharp contacts for two years whereas other radii have but two contacts for two years. In the remainder of the illustrations, similar and additional facts can be ascertained among radial variations, sectional variations, and the relation between tip flushes and diameter flushes.

TABLE 53.—*TTAp 2-4*

	47 cm.	42 cm.	20.5 cm.	5.4 cm.	TF
1938	1 sce 1 msce	1 sce			2
1939	1 sce 1 sL	1 sce 1 sL 1 L	2 sce ddw	2 sce ddw	1

The increment for 1938, *TTAp 2-4* (table 53), insofar as it is present at 47 cm., has one growth layer sharp around the entire circuit

and a second, sharp over more than half the circuit. On some radii, therefore, both contacts are sharp, whereas on others, one is sharp and one is diffuse, the latter of course being an obvious "double." The two growth layers correspond to two tip flushes. In contrast, the increment for 1939, with two sharp contacts throughout, has one tip flush.

The sections of TTC 1-11 (table 54) were cut November 24, 1945; this gives nine years of record. In sections at 244 cm., the nine increments contain 19 sharp contacts, or, counting simply the sharp, complete, entire growth layers and the wholly sharp lenses, they contain 16 sharp, complete growth layers and these represent nine years. The maximum number of growth layers sharply bordered in whole or in part is 29 in sections at 244 cm. Five additional are completely diffuse and, under the microscope, would readily reveal their intra-annual character.

It is also worthy of note that the complexity of the growth-layer display in general decreases outward on the branch, from 244 cm. to 30 cm. from the tip.

Correlation of growth layers from section to section, as between 244 cm. and 212 cm., is especially difficult. Consider 1940. Which intra-annual at 244 cm. corresponds to the half-lens at 212 cm.? At 132 cm., in 1940, all intra-annuals have disappeared, not because they have been cut out longitudinally by the pith (1939 surrounds pith at 132 cm.) but because they actually have been terminated, leaving the annual increment as one sharp, complete, entire growth layer.

The increment for 1945 at 30 cm. contains an overlapping lens.

Variations along a branch, such as TTC 1-11, are well shown by comparing figure 1 of plate 5 with figure 2 of plate 5 and figure 1 of plate 6, and these with figure 2 of plate 6 and figure 1 of plate 7.

The sections of TTC 33-9 (table 55) were cut from the tree January 1, 1943. In 1942, at 49.5 cm., the outermost lens of the three sharp lenses is concurrent. Note that the sections at 49.5 cm. have seven sharply bordered growth layers for three years, growth layers which carry no distinguishing intra-annual character except that some of them are partial. The increment for 1942 does not change its complexity outward on the branch, but it does change its nature to a considerable extent.

The long lens of 1939 in TTC 34-1 (table 56) becomes an entire growth layer outward on the branch, but it does not follow of course that the lens disappears inward, or if it does, that it does not reappear even farther down the branch. In 1940 the lens becomes longer outward. Artificial freezing on May 18, 1941, killed the cambium out-

TABLE 54.—*TTC 1-II*

	244 cm.	212 cm.	132 cm.	78 cm.	30 cm.
1937	1 sce 1 sL	1 sce			
1938	1 sce 2 s arcs	1 sce 1 dce 1 sL			
1939	1 sce 1 sL 4 psL 1 d $\frac{1}{2}$ L	1 sce 2 psce	1 sce		
1940	1 sce 2 psL 1 dL 1 s arc 1 d arc	1 sce 1 s $\frac{1}{2}$ L	1 sce		
1941	1 sce 2 sL 1 psL 1 dL	1 sce ddw	1 sce 2 dce	1 sce 1 sL	
1942	1 sce 2 psL	1 sce 1 msce 1 psL	1 sce 2 psce	1 sce 1 msL	
1943	1 sce 1 sL 1 dL	1 sce 2 s $\frac{1}{2}$ L 1 d arc	1 sce 1 psL 2 d $\frac{1}{2}$ L	1 sce 2 s $\frac{1}{2}$ L	1 msce
1944	1 sce 1 sL	1 sce 1 sL 1 s $\frac{1}{2}$ L	1 sce 2 psL 1 s $\frac{1}{2}$ L	1 sce 2 sL 2 d arcs	1 sce 1 sL
1945	1 sce 1 sL 1 psL	1 sce 3 sL	1 sce 2 psL	1 sce 3 psL	1 sce 2 psL 1 dL

right from 43.5 cm. outward. At 48.5 cm., 5 cm. inward from the freezing apparatus, the cambium suffered some injury; nevertheless, weak densewood was formed. Substantial growth had been made over the whole branch by May 18 and, from 43.5 cm. outward, the

TABLE 55.—TTC 33-9

	49.5 cm.	34.5 cm.	24 cm.
1940	I sce I sL I dL	I sce I msce	
1941	I sce	I sce	I sce
1942	I sce 3 sL	I sce I msce I psL I dL	I sce I dce I psL I dL

TABLE 56.—TTC 34-1

	48.5 cm.	43.5 cm.	37 cm.	29 cm.
1939	I sce I sL	I sce I sL	I sce I msce	I sce I psce
1940	I sce I sL	I sce I sL	I sce I sL	I sce I sL
1941	I sce	inc	inc	inc

TABLE 57.—TTC 34-4

	62 cm.	57 cm.	50 cm.	38.5 cm.
1937	I msce I sL	I msce I sL	I sce	
1938	I sce I psce I sL	I sce I psce I sL	I sce	I sce
1939	I sce I sL	I sce I sL	I sce	I sce I sL
1940	I sce I sL I dL	I sce I sL I dL	I sce I sL	I sce I sL
1941	I sce psg (?)	inc	inc	inc

one-quarter of the growth-layer thickness which was immature at the time of freezing remained so until the branch was cut off November 29, 1941.

Again, in TTC 34-4 (table 57), the formation of xylem was nearly

complete when the branch was frozen artificially on May 18, 1941. This is judged by the thickness of the xylem for 1941.

Multiplicity decreases outward on the branch.

TABLE 58.—*TTC 34-5*

	50.5 cm.	42.5 cm.	35.5 cm.	27.5 cm.
1937	I sce ddw	I msce ddw	I sce	
1938	I sce 2 psce	I sce 2 psce	I sce	I sce
1939	I sce I msce I dL	I sce I msL I dL	I sce I msce or long psL	I sce ddw
1940	I sce I sL	I sce I sL	I sce I sL	I sce I sL
1941	I sce	inc	inc	inc

TTC 34-5 (table 58) was frozen artificially May 18, 1941, and was cut from the tree November 29, 1941. Multiplicity decreases outward in general. In 1939, the mostly sharp, complete, entire growth layer at 50.5 cm. changes to a mostly sharp lens at 42.5 cm.; to a mostly sharp, complete, entire growth layer or a long lens at 35.5 cm.; and to divided densewood at 27.5 cm. The situation of 1939 at

TABLE 59.—*TTC 34-10*

	45 cm.	34 cm.	26 cm.
1940	2 sce	2 sce	I sce
1941	I sce I psL	I sce	I sce ddw
1942	I ce	I ce	I ce

TABLE 60.—*TTC 34-11*

	43.5 cm	30.5 cm.	21.5 cm.
1940	2 sce	I sce	
1941	I sce	I sce	I sce
1942	I sce psg	I msce psg	inc

35.5 cm. is of interest because some of the sections show a mostly sharp, complete, entire growth layer, whereas others show a long, mostly sharp lens. In the 1940 increment, at 35.5 cm., the lens is concurrent.

Many more branches than those analyzed in tables 59 and 60 could

be described from tree TTC 34. The 1940 increment commonly contains two sharp, complete, entire growth layers. Because of the cutting date, July 28, 1942, and the impact of artificial freezing, 1942 may be incomplete. In the 1942 increment of TTC 34-11 (table 60), the postseasonal growth at 43.5 cm. consists of a few cells scattered around the circuit outside the completed growth layer and beneath the cambium. At 30.5 cm. the postseasonal growth consists of one long, incomplete lens made up of one to five rows of large, immature, lightwood cells. The entire growth layer, which at 43.5 cm. is complete and sharply bordered, has a portion of its band of densewood composed of large cells that lack a sharp border on the outside. Here we see the formation of what later would be called a partly sharp, partly diffuse growth layer or a mostly sharp, complete, entire growth layer. Outward on the branch at 21.5 cm. no densewood had been formed by July 28. Growth which was divided into two diameter flushes inward on the branch was combined into one flush outward.

TABLE 61.—TTC 34-26

	54.5 cm	42.5 cm.	34 cm.
1940	I sce		
1941	I sce	I sce	I sce
1942	2 psce inc	2 psce inc	3 dce inc

Branch TTC 34-26 (table 61) was cut from the tree July 28, 1942. At 54.5 cm. the number of sharp contacts varies on different radii from two to four. Among the intra-annuals of 1942, at 42.5 cm., the sharp portion of one parallels the diffuse portion of the other. The total increment of 1942 becomes thicker outward on the branch. Artificial frost was applied to the branch on May 29 at the time the incomplete growth layer was being formed.

TABLE 62.—TTC 35-2

	18 cm.	14 cm.	8 cm.
1944	I sce	I sce	I sce
	I psce inc	I dce inc	inc

Specimens TTC 35-2, 4, and 8 (tables 62-64) were cut from the tree July 31, 1944. Contacts increase in diffuseness outward on the branches, and the incomplete growth layers are in the nature of post-seasonal growth.

Tree TTC 36 (tables 65, 66), insofar as the sample branches are concerned, does not show quite the consistency of the previously described trees. Multiplicity and sharpness of boundary tend to increase slightly, inward on the branches.

TABLE 63.—TTC 35-4

	21 cm.	16 cm.
1943	I sce	I sce
1944	I msce	I msce
	I dce	I dce
	I arc	I arc
	inc	inc

TABLE 64.—TTC 35-8

	21 cm.	14.4 cm.
1944	3 dce	I dce
	inc	psg

TABLE 65.—TTC 36-2

	48.5 cm.	38.5 cm.	24 cm.
1940	I sce	I sce	
1941	I sce	I sce	I sce
	I dL	I dL	I dL
	I s arc	I s arc	I s arc
1942	I sce	I sce	I sce
	I psL	I psL	I psce
	I s arc		

TABLE 66.—TTC 36-4

	50 cm.	38 cm.	26.5 cm.
1940	I sce	2 sce	
	I sL		
1941	I sce	I sce	I sce
		ddw	I psce
1942	I sce	I sce	I sce
	I msce	I psce	I psce

Branch TTJ 1-1 (table 67) was cut off January 11, 1940. In 1937 the intra-annual becomes sharper outward, whereas the densewood of the annual becomes less sharp. *The increment for 1937 is so commonly multiple in the Lubbock region that it can be used as a diagnostic dating feature.* Growth-layer sequence changes decidedly along the length of the branch. At 24 cm., in 1939, thin cells occur inter-

mittently around the circuit and constitute the only evidence of the place where the intra-annual growth layer exists at 44.5 cm.

The juniper branch TTJ 2-1 (table 68) was cut off the tree February 29, 1940. Multiplicity is a bit more prevalent inward on the branch. In the 1936 increment the lens is concurrent. Compression wood just outside the contacts of the mostly sharp, complete, entire growth layers obscures the contacts for a short arc on the inner section but not on the outer. In the 1938 increment, on the inner section,

TABLE 67.—TTJ 1-1

	80 cm.	61 cm.	44.5 cm.	24 cm.
1937	I sce I dce I s arc	I sce I psce	I sce	
1938	I msce	I sce	I sce I dce	I sce
1939	I sce	I sce 2 sL I dL psg	2 sce I d arc psg	I sce psg

TABLE 68.—TTJ 2-1

	Inner	Outer
1936	I sce I psL	I sce
1937	I msce 2 psce	I sce I psce I d arc
1938	I msce ddw	I sce
1939	I sce I psce I dce psg	I sce psg

the densewood shows a distinct tendency for lensing. It gives rise to an interesting situation on the outer section. The densewood, for an arc of 5°, contains a row of cells whose lumens are slightly larger than those of contiguous cells—such is the appearance under high power. Under low power, the row of cells is so nearly invisible that it would in all probability be disregarded by the average student. In contrast, under low-low power it appears to be a genuine lens, difficult to see clearly, it is true, but amply justifying such an interpretation.

TTJ 2-7 (table 69) was cut off the tree January 1, 1943. Here, again, the intra-annuals become more diffuse and weaker outward on the branch.

TABLE 69.—*TTJ 2-7*

	49.5 cm.	38.5 cm.	25.5 cm.
1940	2 msce	2 msce	1 msce 1 dce
1941	1 sce 1 psce	1 sce 1 dce	1 sce 1 dce
1942	1 sce 1 sL	1 sce	1 mspce

TABLE 70.—*TTJ 2-9*

	74.5 cm.	57 cm.	46 cm.
1940	1 sce 1 msce	1 sce 1 sL	
1941	1 sce	1 sce	1 sce
1942	1 pce	1 pce 1 s arc	inc

In TTJ 2-9 (table 70), cut off June 10, 1942, the intra-annuals decrease in area outward on the branches. In contrast, a lens of 1942 in TTJ 2-10, cut off January 1, 1943, becomes an entire growth layer outward.

TABLE 71.—*TTJ 2-12*

	46 cm.	35 cm.	33 cm.	22 cm.
1940	2 sce	2 sce	2 sce	
1941	1 sce 1 dL ddw	1 sce	1 sce	1 sce

The lightwood of the outer growth layer of 1940 in TTJ 2-12 (table 71) varies from one to four cells in thickness. Its densewood is thin and weak compared with that of the inner growth layer. As in many other cases, the "outer thin" growth layer, although sharply bordered, would not be given preference as an annual contact over the inner growth layer if a choice were necessary. To consider the two growth layers as separate annuals would be quite erroneous.

The densewood of 1941 at 46 cm. shows slight separation at two places, the ddw.

The series of branches TTP 20-22 to 40 (tables 72-84) was cut off the tree November 11, 1944, and the amount of tip growth for 1944 was measured November 14, 1944. On all branches, tip growth had been measured January 30, 1943, February 5, 1944, and November 14, 1944. Sections were cut, in all cases, from the measured tip flushes.

In table 72 the entire growth layer and the lens are represented by one tip flush only.

TABLE 72.—TTP 20-22

	5.3 cm.	1.8 cm.	TF
1944	1 sce 1 sL	1 sce	1

TABLE 73.—TTP 20-23

	2.6 cm.	0.8 cm.	TF
1943	1 sce		1
1944	2 sce inc	2 sce	1

A wide-field binocular revealed two, possibly three, growth layers on unstained sections of TTP 20-23. Sections at 2.6 cm. (table 73) were cut from the middle of the 1943 tip growth and those at 0.8 from the middle of 1944. In 1943, one diameter flush corresponds to one tip flush, whereas in 1944 two diameter flushes plus (at 2.6 cm.) an incomplete growth layer correspond to a *single* tip flush. The densewood of the outer sharp, complete, entire growth layer is followed by two to three rows of large-lumened, rather heavily lignified cells which make the outer margin of the xylem indefinite under the cambium and indicate that another growth layer was in process of formation, and was not complete, when growth ceased for the year. Without doubt this "added," or postseasonal, growth would be considered a part of the 1945 increment had the branch been cut off a year or more later. The significance of such mistaken dating of xylem formation is immediately apparent when, for any interpretative purpose whatsoever, the amount of xylem formed in a certain year is measured with a high degree of accuracy. Whether the postseasonal growth increases or decreases inward on this branch is unknown; the significance of the fact is that incomplete growth layers (i.e., lacking densewood) can be formed as the final growth of a season.

Because of the significance to studies of tree growth, three points will be summarized here, points which are illustrated by a great many of our specimens.

(1) TTP 20-23, among many others, gives absolute proof of *two* sharp, complete, entire growth layers for *one* year, 1944, by exact measurement of tip growth both before and after the growth occurred. In TTP 20-22, one of the 1944 growth layers is a sharp lens. If one used sharpness of margin as a criterion of annual character, or if one "counted" growth layers for one reason or another, he would have three "annual" growth layers formed in two years.

(2) TTP 20-23 demonstrates that a growth layer does not necessarily have to stop its growth at a certain time and mark that cessation by cells with a certain standard set of features such as narrow, thick-walled, and heavily lignified. Had this branch been cut off the tree two years later than it actually was, would the outer margin of 1944 increment have been identifiable?

(3) So-called "postseasonal growth" varies in amount all the way from an isolated cell here and there to an entire but incomplete growth layer and even to an entire, complete growth layer. Any one of the variations leads to confusion and actual uncertainty as to the exact position of the outer margin of the annual increment. In TTC 12-14-a, at 178 cm., the outer border of 1945 (branch cut off November 17, 1945) is irregular because some of the radial rows of cells protrude outward farther into the cambial region than the row or rows immediately adjacent. Such irregularity is common. The outer border of 1945 in sections *b* (pls. 10, fig. 2; 11, fig. 1), at 147 cm., is highly irregular, partly sharp and partly diffuse by locally added large-lumened, thick-walled cells. In sections *f*, at 27.5 cm., the outer margin is made strikingly indefinite by added large-lumened, thin-walled, immature cells. At 16 cm., in sections *g*, the outer border is once again only slightly irregular, as it is 178 cm. from the tip of the branch. These different types and amounts of "postseasonal growth" would have been identified as having been formed the following year if the branch had been cut off a year or so later, or would have masked the true position of the annual contact. Another point is brought out by the immature postseasonal growth of TTC 12-14-f. If the branch had not been cut off when it was, the immature cells either would have been lignified the next season or would have remained immature and thus resembled many observed cases of zones of immature cells extending partially or completely around the circuit.

Hidden annual contacts and misdated xylem add a factor of uncertainty to any studies based upon exact measurement of xylem supposedly formed in any one year.

Although TTP 20-24 (table 74) was cut off November 11, 1944, the densewood at 3.7 cm. was weakly developed. This branch gives an example of a lens appearing outward on the branch.

TABLE 74.—TTP 20-24

	3.7 cm.	0.9 cm.	TF
1944	1 sce	1 sce 1 dL	1

TABLE 75.—TTP 20-25

	3.8 cm.	1.8 cm.	0.5 cm.	TF
1943	1 sce			1
1944	2 sce	2 sce	1 sce	2

In TTP 20-25 (table 75), in contrast with TTP 20-22 and 23, each diameter flush of 1944 is represented by one tip flush. Thus at 3.8 cm., the branch has three tip flushes for three diameter flushes for two years. No doubt can exist as to the time the diameter and tip flushes were formed.

The densewood of 1943 is thin and weak. For 1944, at 3.8 cm., the densewood of the outer growth layer is weak, whereas that of the inner growth layer is very strongly developed; at 1.8 cm., the two bands of densewood are equally developed; at 0.5 cm., the densewood of the outer growth layer (the only one present because the section was taken from the second or outer tip flush) is thin, weak, and poorly developed.

Multiple growth layers in an annual increment and the unequal development of densewood, strong on intra-annuals and weak on annuals, constitute phenomena which would have made dating wholly uncertain had not tip growth been measured.

The densewoods terminating the annual increments in TTP 20-26 are weak on all sections, whereas that of the intra-annual of 1944 is strong. With the one sharp, complete, entire growth layer of 1943, TTP 20-26 can be analyzed as three diameter flushes for two tip flushes for two years. This contrasts with the analysis of TTP 20-25 which comes out as three diameter flushes for three tip flushes for two years.

Sections at 2.7 cm. in TTP 20-27 (table 76) came from the second tip flush of 1943. The diffuse growth layer of 1943 at 4.9 cm. is extremely faint; in fact, it is suggestive only of the first tip flush of 1943 which is set off from the second flush by a constriction of the branch. It is indeed so faint that one would pass it by had he not

been put on the alert by the two tip flushes. Two years before the stained sections were analyzed under the microscope, an inspection of the unstained sections under a wide-field binocular showed "probably three growth layers." Should it be said that 1943 has two growth layers? Two diameter flushes? Growth was quasi-cyclic in that it slowed down sufficiently to leave some evidence of itself in densewood but not enough to produce a sharply bordered growth layer—it is, of course, a transitional form, a single step in a long series beginning with a scarcely identifiable tendency to form densewood and

TABLE 76.—*TTP 20-27*

	4.9 cm.	2.7 cm.	0.8 cm.	TF
1943	1 sce 1 dce	1 sce		2
1944	1 sce	1 sce	1 sce	1

ending with a sharp, complete, entire growth layer whose intra-annual nature cannot be distinguished from annual except by methods of absolute dating.

The increment for 1944 contains one diameter flush and one tip flush, which is unusual for 1944 in TTP 20. Therefore, analysis gives three diameter flushes for three tip flushes for two years. The years are identical with previous branches, but the flushes are differently located. Or, if we neglect the diffuse growth layer, there are two diameter flushes for three tip flushes for two years, an analysis which, in its way, testifies to multiplicity of tip flushes in a year in exactly the same way that two diameter flushes to a single tip flush testify to multiplicity of diameter flushes in one year.

TABLE 77.—*TTP 20-28*

	11.8 cm.	2.8 cm.	TF
1943	1 sce		1
1944	1 sce 1 psL	1 sce	1

The dating of the growth layers in TTP 20-28 (table 77) is certain because tip growth was measured and because the sections were cut from the measured tip flushes.

Although 1943 growth is described as sharply bordered, it is slightly indefinite over a large portion of the circuit for the reason that the outer four or five densewood cells are weaker and less well lignified than the cells immediately to their interior.

The outer margin of 1944 at 11.8 cm. is rather weak and poorly developed locally; at 2.8 cm. the entire outer margin is weak and irregular.

Since the lens is exterior, it ceases at some point between 11.8 and 2.8 cm. Analysis gives three diameter flushes for two tip flushes for two years. Some radii, of course, show three sharp contacts for two years.

TTP 20-30 has two diameter flushes for two tip flushes for two years and is very nearly the ultimate in simplicity. However, the 1943 increment has several thin arcs of slightly narrower cells buried in compression wood in the lightwood zone. This is taken to represent one of the earliest evidences of growth rhythm as mentioned under TTP 20-27 above.

TABLE 78.—TTP 20-31

(Right branch)

	6.5 cm.	2.7 cm.	0.8 cm.	TF
1943-1944	1 sce	1 sce	1 sce	3

(Left branch)

	7.1 cm.	1.8 cm.	TF
1943	1 sce		1
1944	1 sce	1 sce	1

The sections of TTP 20-31 (table 78) contain a rather curious situation in the two branchlets which arose from the outer end of 1942 tip growth. From the right branch, sections were taken at 6.5 cm. from the middle of the first tip flush of 1943; at 2.7 cm. from the middle of the second tip flush of 1943; and at 0.8 cm. from the middle of 1944 tip growth. No section contains more than one growth layer except for sections at 2.7 cm. which show short arcs of interrupted densewood four to six cells in from the cambium. From the left branch, sections were taken at 7.1 cm. from the middle of the single flush of 1943, and at 1.8 cm. from the middle of 1944 tip growth. Each diameter flush accompanied one tip flush. Such discrepancy between two branchlets which arose from almost exactly the same point, one a terminal and the other a large lateral bud, is difficult to explain. (1) It is possible, but not probable, that the original blocks from which sections were cut became mixed. The slides were compared with the blocks and agreed satisfactorily. (2) The right branch is abnormal in the sense that elongation occurred without corresponding diameter increase. However, the diameter of

the branchlet decreased in each successive tip flush. (3) Or, it might be that the three tip flushes were accompanied by diameter flushes whose outer margins, save that of 1944, cannot be identified. In any event, here in two adjacent branchlets there is a situation not easily explained by the influence of external growth factors, unless it be that the rigorous and variable conditions of the extreme lower forest border promote variable anatomical response throughout the plant body.

TABLE 79.—*TTP 20-32*

	12.9 cm.	4.1 cm.	TF
1943	I sce		I
1944	I sce I dce	I sce	I

In TTP 20-32 (table 79), the diffuse growth layer does not have a tip flush counterpart. The growth layer becomes so diffuse and so weak out at 4.1 cm. that it would be wholly ignored had it not been seen at 12.9 cm. In this case, as in so many others, the intra-annual becomes more definite down the branch.

TTP 20-33 (table 38) was set out previously on page 109. Two tip flushes were formed in 1943, and the sections at 11 cm. came from the first flush, whereas those at 6.5 cm. came from the second. The diffuse growth layer is really an arc whose cusps very nearly unite. Because the arc at 6.5 cm. is very probably the same one present at 11 cm., it cannot represent the first tip flush of 1943. The increment for 1944 in TTP 20-33 is represented by one tip flush. The divided densewood at 11 cm. extends farther around the circuit at 6.5 cm., but whether it becomes the arc at 2.7 cm. is unknown.

TABLE 80.—*TTP 20-35 (twin branches)*

	6.3 cm. 10.1 cm.	1.3 cm. 3.6 cm.	TF
1943	I sce		I
1944	I sce I psce I psL	I sce	I

In January 1943 twin buds were observed on TTP 20-35, and thereafter the resulting twin branches were measured. The growth layers exposed when the two branches were sectioned (table 80) were so completely identical that the above table includes both branches. In the two outer sections (one at 1.3 and the other at 3.6 cm.),

evidences of the intra-annuals of 1944 are so faint that they would be completely disregarded unless one knew them to be present on the inner sections.

TABLE 81.—*TTP 20-36*

	15 cm.	8.5 cm.	4 cm.	TF
1943	I sce I dce	I sce		2
1944	I sce I psce	I sce I dce	I sce I dce	1

Sections at 15 cm. in TTP 20-36 (table 81) came from the middle of the first 1943 tip flush; those at 8.5 cm. came from the middle of the second 1943 tip flush; and those at 4 cm. came from the middle of the 1944 tip flush: In the 1943 increment the inner tip flush corresponds to the one diffuse, complete, entire growth layer, and the outer to the one sharp, complete, entire growth layer. In the 1944 increment one tip flush corresponds to two growth layers. The relations among tip flushes, diameter flushes, and years are apparent.

TABLE 82.—*TTP 20-38*

	9.4 cm.	3.1 cm	TF
1943	I sce I d arc		1
1944	I sce dL's	I sce dL's	1

TABLE 83.—*TTP 20-39*

	8.7 cm.	3.2 cm.	TF
1943	I sce I dce		1
1944	I sce	I sce	1

TTP 20-38 and 39 (tables 82-83) should be contrasted with preceding branches, especially TTP 20-36 (table 81).

Sections at 26 cm. in TTP 20-40 (table 84) were cut from outer

TABLE 84.—*TTP 20-40*

	26 cm.	24.3 cm.	17 cm.	5.2 cm.	TF
1st 1943	I sce	I sce			1
2nd 1943		I sce	I sce		1
1944	I sce dL	I sce I dce	I sce I d arc	I sce	1

end of 1942 tip growth; those at 24.3 cm. from middle of first 1943 tip growth which was 1.4 cm. long; those at 17 cm. from middle of second 1943 tip growth which was 13.3 cm. long; and those at 5.2 cm. from middle of 1944 tip growth. At 24.3 cm. each tip flush of 1943 has a corresponding diameter flush. The diffuse growth layers of 1944 have their densewood buried in compression wood; that is to say, the diffuse lenses at 26 cm. are actually composed of compression wood some of whose cells are sufficiently narrow and continuously oriented to give densewood. At 17 cm., a complete circuit of compression wood contains an arc of narrow cells—hence the designation of one diffuse arc. At 5.2 cm., lenses and arcs of compression wood are present but contain no narrow cells, no hint of intra-annual densewood. Sections at 26 cm. show that simplification occurs inward on the branch.

TABLE 85.—TTP 21-7

	41 cm.	24 cm.	TF
1938	1 msce	1 psce	1
1939	1 sce	1 psce	1
	1 dce	1 dce (faint)	
1940	2 sce	1 sce	1
		1 dce	

The branch, TTP 21-7 (table 85), was cut from the tree November 9, 1940. In 1938, the outer margin of the increment becomes somewhat more indefinite outward on the branch.

At 41 cm. in 1939, the outer growth layer is much thinner than the inner growth layer; in fact, on the short radius, the densewood of the inner growth layer makes contact with the densewood of the outer growth layer. This local absence of lightwood forces the outer growth layer to assume the appearance of a lens which, of course, it is not. The lightwood is lenticular, to be sure, but not so the densewood. A magnification of low amount would be powerless to resolve the 1939 growth layer. At 24 cm., the one diffuse, complete, entire growth layer of 1939 has disappeared except for very slight traces.

The outer growth layer of 1940 at 41 cm. possesses lenticular lightwood, but entire densewood, in much the same fashion as 1939 does. Over a short arc the densewood is made up of one to two cells radially. At 24 cm., the inner growth layer of 1940 has lost its definiteness—it has faded and diffused.

The branch, TTP 21-8 (table 86), was cut from the tree February 1, 1941. At 48 cm. the relation of compression wood to dense-

wood creates a rather unusual phenomenon. Narrowing of cells on the long radius begins far back in the compression wood which itself ceases outward before attaining the outer margin of the growth layer. This outer zone has a translucent appearance and rests halolike on the growth layer.

The increments for 1936 and 1937 have one tip flush each, for a minimum of two distinct diameter flushes. Such a relationship is taken to be one of the criteria of multiplicity.

TABLE 86.—*TTP 21-8*

	48 cm.	22 cm.	TF
1st 1936	1 sce	1 sce 1 dce	1
2nd 1936	1 sce		
1st 1937	1 sce	1 sce 1 sce ddw	1
	1 d arc		
2nd 1937	1 sce		
1938	1 msce	1 sce	1
1939	1 psce	1 sce 1 psce	1
1940	1 sce	1 ce	1

At 22 cm., second 1936 appears to be entirely divided densewood under moderate to high powers of magnification, but under lower power, such as 20X, the appearance is more that of two distinct growth layers. The diffuse arc in first 1937 is simply a tangential row of narrower cells buried in compression wood and better described, perhaps, as interrupted densewood. At 22 cm. the divided densewood listed is part of second 1937. The mostly sharp, complete, entire growth layer of 1938 at 48 cm. appears diffuse for a short distance, under low power, because the amount of lignification on both sides of the contact is the same. High power resolves the nature of the contact. The increment of 1939 at 48 cm. consists commonly of two to three large cells and one to four narrow. Here and there around the circuit, however, these sizes not only approach each other but approach the sizes of those in contiguous growth layers, a gradational feature making recognition of 1939 difficult at those places except under high power.

The increment for 1939 at 22 cm. contains two entire growth layers, the *inner* one of which is sharply bordered around the entire circuit. The *outer* growth layer has an indefinite to diffuse margin

because of its relations to the increment for 1940. Perhaps it is worthwhile to emphasize at this point that under low powers and with an absence of absolute dating, the outer border of the first growth layer of 1939 would be considered an annual border and the true annual margin of 1939 would be identified as an obvious "double" of the next outer growth layer. Under low power the 1940 increment, both at 48 and 22 cm., appears to be a series of concurrent lenses. Under high power it appears to be continuous around the circuit, dwindling, however, to a thickness of one or two rows of narrow cells which lie against the densewood of 1939 and are indistinguishable except by continuous tracing under high power. Lightwood is lenticular in truth, but densewood, and therefore the growth layer, is continuous around the circuit; at no point did the cambium fail to divide.

TABLE 87.—*TTP 22-1*

	5.8 cm.	3.8 cm.	TF
1940	1 sce	1 sce	1
1941	1 sce	1 sce	1
	1 dce	1 dce	

TTP 22-1 (table 87) was cut from the tree January 17, 1942. Dating is certain because of tip-growth measurements. Sections at 5.8 cm. came from the 1940 tip flush, whereas those at 3.8 cm. came from the 1941 tip flush.

Apparently there is an anomalous situation as set out in the above chart—a 1940 increment out in the tip growth of 1941. Because of tip measurements and because of the striking similarity between the sections from 5.8 and 3.8 cm., the dating of the growth layers is considered to be accurate. Sections at 3.8 cm. were cut from the measured tip flush of 1941, it is true, but from within the longitudinal reach of the measured length of the terminal bud (3.2 cm.) as it existed prior to the start of 1941 growth. In other words, if we are correct, a substantial amount of "1941" growth actually was formed in 1940. A growth layer of a previous year is thus found within the reach of the succeeding year's tip growth.

What age should be assigned to the "1940" growth layer included in the 1941 tip flush? Was "1940" actually present in the terminal bud before 1941 growth began? If so, was xylem of "1940" mature before 1941? What are the ecologic implications?

This phenomenon is considered later, on pages 199 and following.

Tree TTP 23 shows rather remarkable consistency of growth-layer patterns among the sections of each branch. In TTP 23-1, 2, 3, and 4, the 1940 increment appears at first sight to be a problem growth layer of great uncertainty. TTP 23-4 (table 88) serves as an example of all these branches. In sections *a*, at 34.5 cm., 1940 has been reduced nearly to a minimum. It appears as divided densewood of 1939 at one or two places, dependent upon the particular section examined. At these places, 1940 consists of one to two rows of large cells and one to two rows of narrow cells. Elsewhere no lightwood is present, only densewood. The reduction has gone so far at some

TABLE 88.—TTP 23-4

	34.5 cm.	21.3 cm.	13.8 cm.
1938	1 msce	1 sce	1 psce
1939	1 msce	1 dce	1 psce
1940	1 ce	1 sce	1 msce
1941	inc L	inc	inc

points that the densewood of 1939 plus all of 1940 consists of two narrow cells, one for 1939 and one for all of 1940. Magnifications of 20X or less do not reveal the presence of 1940—analysis at such powers would no doubt consider 1940 absent. In sections *b*, at 21.3 cm., the 1940 increment is clearly present around the entire circuit. For at least two-thirds of the distance, it consists of one wide cell and two narrow cells; for the other third, it is up to five cells thick. Sections *c*, at 13.8 cm., show 1940, under low power, as a lens covering four-fifths or more of the circuit. High power reveals it as an entire growth layer, densewood being continuous. In addition to the gradual radial reduction of the growth layer near the cusps of the “low-power” lens, there are other irregularities of length in adjacent radial columns of cells; for instance, one wide and one narrow cell make up 1940, or three narrow cells comprise densewood of 1939 plus all of 1940, or one densewood cell makes up all of 1940.

The increment of 1940 is best developed in sections *b* and least developed in sections *a*. If the several wide cells are absent from sections *a*, 1940 would be represented by densewood only and therefore would be indistinguishable from the densewood of 1939. The lightwood of 1941 is so large-celled as to give a striking contrast with all of 1940. If these growth layers were not dated accurately and studied closely under high magnification, some workers might be loath to call 1940 an annual. This applies here as well as to many

other specimens. And such supposed omission of growth layers would merit the conclusion that the cambium had lain dormant for more than a calendar year. Our studies indicate, however, that the cambium was sluggish, very sluggish, but not dormant for such a long interval. As a matter of fact, the cambium varies in its activity among different branches of TTP 23; in some it was very active, in others it was sluggish. The variable activity applies longitudinally on any one branch, as on TTP 23-4, and also around the circuit of any one section.

The branches TTP 23-5 to 23-20, measured for two years and cut November 11, 1944, are rather simple compared with TTP 20, for instance, and resemble each other to a remarkable degree. With one exception, 1943 contains one growth layer whereas 1944 is almost universally multiple. The intra-annuals of 1944 invariably fade and weaken outward on the branch. In all instances, each year contains one tip flush, except in TTP 23-9.

TABLE 89.—TTP 23-9

	7 cm.	4.3 cm.	1.8 cm.	TF
1943	1 sce	1 sce		2
1944	1 sce d arcs	1 sce 1 dce	1 sce 1 dce	1

One diameter flush represents two tip flushes in 1943 for TTP 23-9 (table 89). The growth layer at 4.3 cm. in 1943 has a feeble and weak outer contact.

Branches TTP 24-1 to 24-4 were cut from the tree November 29, 1941.

TABLE 90.—TTP 24-1

	43 cm.	33 cm.	23 cm.
1938	1 sce	1 sce	
1939	1 msce	1 sce	1 sce
1940	1 msce 1 psce 1 sL	1 sce 1 dce 1 sL 1 dL	1 sce
1941	1 sce	inc	inc

The sharp lenses of 1940 at 43 and 33 cm. in TTP 24-1 (table 90) are both concurrent and are interior in that they come at the start of the annual increment. In contrast, the diffuse lens comes at the outer

margin, thus giving us a comparatively rare case of both interior and exterior lenses in the same annual increment. At 33 cm. the concurrent lenses are narrower and reduced in number from the sections at 43 cm.

The branch was frozen artificially at 33 cm. on May 25, 1941, at which time the increment was as wide as, or wider than, that for 1940. Apparently no growth occurred after May 25, at 33 or 23 cm., that is outward on the branch from the portion frozen. At 43 and 33 cm. the cambium was almost wholly dead save for a cell here and there containing protoplasm or a nucleus. In contrast, the cambium at 23 cm. contained protoplasm nearly around the circuit. Although not active, the cambium certainly was not dead. The growth layer at 43 cm. either began to form earlier than it did farther outward, or formed more rapidly, or went on to completion after freezing occurred outward on the branch. The densewood at 43 cm. of 1941 was only feebly lignified.

TABLE 91.—TTP 24-2

	47.5 cm.	43 cm.	39 cm.	29 cm.
1937	I sce I dce	I sce	I sce	
1938	I sce	I sce	I sce	I sce
1939	I sce	I sce	I sce	I sce
1940	I sce I msce	I sce I psce	I sce 2 dce	I sce 2 dce
1941	I dce inc	inc	inc	inc

It is probable that the increment labeled 1937 in TTP 24-2 (table 91) represents but the second half of 1937, the inner sharp, complete, entire growth layer, not listed, being the first half. In 1940 the intra-annuals become fainter outward. The branch was frozen artificially on May 25, 1941.

Although 1935 in TTP 24-3 (table 92) is designated "sharp, complete, entire" at 35.5 cm., its growth layer was not as definite as at 42 cm. The sections at 30 cm. came from the middle portion of the branch length which was subjected to artificial freezing May 25, 1941. Sections at 35.5 cm. were cut in sequence outward from that portion of the branch which lay within the rubber gaskets of the freezing apparatus, the two columns of the table representing the inner and the outer sections. The growth layer "diffuse, complete, entire" of first 1936 at 30 cm. possesses as definite a contact as the

one "sharp, complete, entire" although it appears to be indefinite because of the feeble development of the lightwood immediately to the outside. On unstained sections under very low magnifications the outer boundary of 1937 appears to be diffuse. Examination of stained sections under the microscope shows that the densewood of 1937 is definite and the boundary sharp but obscured by severe frost injury almost at the start of 1938.

TABLE 92.—*TTP 24-3*

	42 cm.	35.5 cm.	35.5 cm.	30 cm.	20 cm.
1935	1 sce	1 sce	1 sce		
1st 1936	1 sce	1 sce	1 sce	1 sce	
			1 dce	1 dce	
2nd 1936	1 sce	1 sce	1 sce	1 sce	
	1 dce	1 dce	1 dce		
1st 1937	1 sce	1 sce	1 sce	1 sce	1 sce
2nd 1937	1 sce	1 sce	1 sce	1 sce	1 sce
1938	1 dce	1 dce	1 dce	1 sce	1 sce
1939	1 msce	1 msce	1 msce	1 sce	ddw
1940	1 msce	1 msce	1 msce	1 msce	1 msce
1941	1 msce	1 msce	1 msce	1 sce	1 sce
	1 pcL	1 pcL	1 pcL	inc L	inc L

The outer contact of 1938 is made obscure by the subnormal development of 1939. At first sight, at 42 cm., and under very low powers, 1939 is a concurrent lens of two members. Under higher powers, the lightwood only of 1939 is lenticular, the densewood, two cells thick, lying flush against the densewood of 1938 and continuing between the cusps of the "lenses." Lightwood is lenticular, densewood entire. At 30 cm. the resolution of 1939 requires high power on stained sections, but even so, one would remain in doubt if he did not have other branches from the same tree available for study. The increment at 20 cm. is an excellent example of divided densewood constituting total annual growth. The densewood of 1939 lies immediately against that of 1938 over most of the circuit; where it does not do so, the insertion of partially developed lightwood cells makes 1939 visible under low power for half the extent of those cells. It is an interesting point to note that one of the "lenses" of 1939 carries a natural frost injury.

The apparent, as against the actual, occurrence of 1939 brings out a possible contrast in interpretations. Under very low power the

growth layer for 1939 apparently consists of restricted lenses and, if soil moisture is considered to be the dominant growth factor in the extreme lower forest border, such a growth layer would indicate a very dry growing season. With high magnification, however, the growth layer for 1939 is seen to be entire and would indicate restricted moisture. The cambium had limited activity but was not dormant over much of the circumference of the section throughout an entire growing season. Other branches of the same tree show normal development for 1939. Such variations in one annual increment may, and do, occur from tree to tree in the same general area, as was mentioned in connection with tree TTP 23. Care must be exercised, apparently, before general ecologic or climatic conclusions are drawn.

The increment of 1940 in TTP 24-3 has a sharp outer contact except where followed by an interior lens of 1941. Over a very short arc at 42 cm., 1940 is reduced to two or three rows of densewood cells lying against the densewood of 1939 which, in turn, lies against the densewood of 1938.

The increment of 1941 is atypical because of artificial freezing. It consists of interior and exterior concurrent lenses. Natural frost injury in the interior lenses apparently dates them. Here again, it is the lightwood that is lenticular—the growth layer is entire. The outer growth layer consists of lenticular lightwood whose completion was prevented by artificial freezing. Outward on the branch the incomplete lens becomes thin and faint.

TABLE 93.—TTP 24-4

	49 cm.	47 cm.	41.5 cm.	29 cm.
1937	1 sce	1 sce	1 sce	
1938	1 sce	1 sce	1 sce	1 sce
1939	1 sce	1 sce	1 sce	1 sce
1940	1 sce	1 sce	1 sce	1 sce
	1 psce	1 psce	1 psce	
				2 dce
	1 dce	1 dce	1 dce	
1941	1 sce	inc	inc	inc
	1 sL			

TTP 24-4 (table 93), in contrast with 24-1, 2, and 3, has comparatively thick growth layers. What is labeled "1937" in TTP 24-4 is probably second 1937. Buried within the densewood of 1938, at 49 cm., there is a faint discontinuous band of narrow cells—interrupted densewood. At 29 cm. the 1938 growth layer contains circles of compres-

sion wood with which slightly narrower cells are associated. The lightwood of 1939, at 29 cm., contains arcs of narrower cells; compression wood is associated with one of the arcs. In general, the annuals of 1940 become sharper outward on the branch whereas the intra-annuals become more diffuse. The sharp lens of 1941, at 49 cm., is exterior. Apparently the increment went on to completion in spite of the artificial frost applied outward on the branch May 25, 1941. Frost injury is, of course, responsible for the state of 1941 at 47 cm. and outward.

The increment for 1941 gives proof of multiplicity and strongly suggests that the sharp lens was formed after May 25 and before the branch was cut November 29, 1941.

TABLE 94.—TTP 24-10

	49 cm.	36 cm.	26 cm.	TF
1938	I sce	I sce	I sce	I
1939	I sce	I sce	I sce	I
1940	I sce	I sce	I sce	I
	I psce	I psce		
			2 dce	
	I dce	I dce		
1941	I sce	I sce	I sce	I
	I sL	I sL (weaker)		
1942	I sce	I sce	I sce	I
			I gl (ddw)	

Branches TTP 24-10 to 24-16 were cut from the tree January 1, 1943. In the 1940 increment of TTP 24-10 (table 94), the intra-annuals weaken outward to such an extent that they are barely visible at 26 cm. The sharp lens of 1941 is concurrent, interior, and undoubtedly caused by a late spring frost which is intimately associated with it. At 36 cm. the lens is weak. The intra-annual of 1942 at 26 cm. is labeled "growth layer" by reason of the fact that its densewood merges with that of the annual for part of the circuit, separates from the annual densewood to make divided densewood for another portion of the circuit, and for 60° is separated sufficiently far to make a lens.

Branch TTP 24-11 resembles branch 24-10 in many details except that, in 1940, one of the intra-annuals appears as divided densewood rather than as a discrete growth layer.

In 1937 of TTP 24-12 (table 95), the densewoods of the intra-annuals are buried in compression wood. The extra growth layer of 1942 at 40 cm. varies from merged densewood, to divided densewood, to a lens. Where the densewoods are merged, the inner margin is extraordinarily sharp, and where they divide, the inner margin of the inner band of densewood is sharper than its outer margin. The tip flush for 1942 contains two zones without needles and two zones with needles; that is to say, two sets of bare-needle zones.

TABLE 95.—TTP 24-12

	53.5 cm.	40 cm.	30.5 cm.	TF
1937	1 sce 2 dce			I
1938	1 sce	1 sce		I
1939	1 sce	1 sce	1 sce 1 psce	I
1940	1 sce 1 psce	1 sce 1 dce	1 sce 1 dce	I
1941	1 sce	1 sce	1 sce	I
1942	1 sce	1 sce 1 psce or ddw	1 sce 1 dce	I

TABLE 96.—TTP 24-13

	53 cm.	41 cm.	30 cm.	TF
1938	1 sce	1 sce		I
1939	1 sce	1 sce	1 sce	I
1940	1 sce 1 psce	1 sce 1 dce 1 sL	1 sce 1 dce 1 sL	I
1941	1 sce	1 sce	1 sce	I
1942	1 sce ddw psg	1 sce 1 dL	1 sce 1 dL	I

Intra-annuals of TTP 24-13 (table 96) become fainter outward on the branch. Two sets of bare-needle zones are present in the tip growth of 1942. In 1942, the divided densewood becomes a single lens at 41 cm. and concurrent lenses at 30 cm. The postseasonal growth occurs as very narrow, short, incomplete lenses.

In the increment of 1939 for TTP 24-15 (table 97) at 37 cm., narrow cells accompany arcs of compression wood, a combination which occurs so often as to suggest a relationship. The divided densewood of 1942 at 52 cm. covers but a very short arc, whereas at 37 cm. it covers fully 180° of circuit. Tip growth of 1942 contains two sets of bare-needle zones.

TABLE 97.—TTP 24-15

	52 cm.	37 cm.	25 cm.	TF
1938	I sce	I sce		I
1939	I sce	I sce		I
1940	I sce I psce	I sce I dce	I sce idw	I
1941	I sce	I sce	I sce	I
1942	I sce	I sce	I sce 2 dce	I
	ddw	ddw psg	psg	

TABLE 98.—TTP 24-16

	47 cm.	35 cm.	26.5 cm.
1939	I sce	I sce	
1940	I sce I dce	I sce I dce idw	I sce idw
1941	I sce	I sce	I sce
1942	I sce	I L inc	inc

TABLE 99.—WCh 2-6

	45.8 cm.	28.7 cm.	TF
1944	I sce 2 dce	I sce	2
1945	I sce	I sce I dce	I

The branch TTP 24-16 (table 98) was killed by artificial freezing May 16, 1942. Isolated arcs of narrow cells typify 1940 and suggest a rhythmic pattern. Compression wood commonly shows the same rhythm. In 1942 at 35 cm., the lens was formed after artificial freezing by a regenerated portion of the cambium.

Branch WCh 2-6 (table 99) was cut from the tree June 17, 1945.

Sections at 45.8 cm. came from the first tip flush of 1944 which was approximately 20 cm. long ; sections at 28.7 cm. came from the second tip flush of 1944 which was 2.8 cm. long. About one-third of the way out in the 1944 increment at 45.8 cm. there occurs one of the diffuse growth layers, whereas seven-eighths of the way out there is a second one, undoubtedly corresponding to the second tip flush. The inner growth layer records a variation of cambial and physiological activity unrecorded in the tip growth. Since a wide-field binocular revealed only three growth layers rather than the four actually present, unstained sections under low power cannot yield an ecologic picture as complete as do stained sections under a microscope. The diffuse, complete, entire growth layer in 1945 was made by a late spring frost.

TABLE 100.—*WCh 3-1*

	36 cm.	9 cm.	TF
1944	1 sce	1 sce	1
	1 d arc	1 gl	

WCh 3-1 (table 100) was cut from the tree January 21, 1945. The extra growth layer at 9 cm. has an indefinite outer margin. Insofar as relative position is concerned, the growth layer corresponds to the arc at 36 cm.

TABLE 101.—*XSC 1-1*

	81 cm.	68 cm.
1932	2 sce	1 sce
	1 psce	
1940	1 sce	1 sce
		3 sL
		1 s ½L
	ddw	
	inc	inc

One of the sharp lenses is overlapping at 68 cm. in *XSC 1-1* (table 101). The branch was frozen artificially April 8, 1940, and was cut off May 10, 1940. The 1940 increment at 68 cm. is illustrated in text figure 15, which shows a compound lens, an overlapping lens, and a half-lens between the inner complete, entire growth layer and the outer incomplete, entire growth layer. For the most part, the incomplete growth layer in 1940 consists of frost-injured and recovery xylem. It is of moment to note the amount of xylem formed not only before May 10 but also probably before April 8.

Branch XSC 1-2 (table 102) was frozen artificially at 107 cm. on April 8, 1940, and was cut from the tree May 10, 1940. The variations along the branch are only too apparent—although they are ex-

TABLE 102.—XSC 1-2

	107 cm.	89 cm.
1932	2 sce	2 sce
	1 sL	1 psce
	1 msL	
1933	2 sce	2 sce
	1 s $\frac{1}{2}$ L	1 psL
		1 s $\frac{1}{2}$ L
		3 ddw
1934	1 sce	2 sce
	dL's	
		1 d arc
1935	2 sce	3 sce
	2 sL	1 psL
1936	1 sce	4 sce
	2 msce	
	1 sL	5 sL
1937	2 sce	2 sce
	1 sL	2 sL
		1 msL
	2 psL	1 psL
	1 sL	
	2 d $\frac{1}{2}$ L	3 d $\frac{1}{2}$ L
	1 s $\frac{1}{2}$ L	1 s ddw
	ddw	
1938	1 sce	1 sce
	1 psce	1 dL
1939	2 sce	1 sce
	1 sL	3 sL
	1 msL	1 dL
	1 s $\frac{1}{2}$ L	1 s $\frac{1}{2}$ L
		2 d $\frac{1}{2}$ L
	1 d arc	
1940	inc L	inc

treme, they seem to be typical of Arizona cypress at the extreme lower forest border. Following are notes concerning the annual increments.

1932, at 107 cm.—The inner sharp, complete, entire growth layer, two-thirds to four-fifths of the entire increment, bears heavy compression wood, thus contrasting sharply in color with the outer sharp,

complete, entire growth layer free of compression wood. The mostly sharp lens covers an arc of 270° . At its widest part, the densewood of the lens is divided into two sharply bordered bands which actually are transitional between divided densewood and a short, sharp lens.

1933, at 107 cm.—The inner sharp, complete, entire growth layer makes up most of the increment. Traced around the circuit the two sharp, complete, entire growth layers vary in relative thicknesses. At 89 cm.—The inner sharp, complete, entire growth layer contains an exterior lens of 200° whose densewood, near one cusp of the lens, divides into three bands making doubly divided densewood. These are resolved only under high power. However, the cells of the outer band of densewood grade tangentially into wider and wider cells until there is a complete transition from divided densewood of the inner growth layer to a sharp half-lens within the interior of the outer growth layer. The outer growth layer itself also contains divided densewood.

1934, at 107 cm.—Increments for 1934 and 1935 are separated with difficulty. Actually there are five to eight growth layers in the two years. On the short radius, 1934 is single. The long radius contains a decided bulge made up of several diffuse lenses. Thus cambial activity, locally rapid, is decidedly rhythmic. Many bulges among our specimen branches are built up by series of half-lenses facing each other. Careful search with high power shows that the densewood of the half-lenses in many cases can be traced tangentially across the bulge to their counterparts on the other side. The narrowness and sharpness of the lenses at and near their cusps suggest not so much differential cambial activity within the active area as the completeness and duration of cambial inactivity and maturation processes which become progressively less when traced from cusp point inward tangentially to mid-lens.

1935, at 107 cm.—Each of the sharp, complete, entire growth layers contains a long, sharp, exterior lens. In contrast with 1932, as well as with numerous examples in other branches and trees, the outer sharp, complete, entire growth layer makes up the main bulk of the 1935 increment. At 89 cm.—The increment for 1935 is set off from that of 1934 chiefly on a color basis—the separation is necessarily uncertain because 1935 can have no frost and because of multiple sharp, complete, entire growth layers in both years. It is set off from 1936 by typical frost injury at the start of 1936. On the long radius, the inner sharp, complete, entire growth layer has a sudden bulge, part of which is due to a 120° exterior lens. Just outside this lens the middle sharp, complete, entire growth layer contains an

interior lens made up entirely of compression wood whose outer cells are narrow for half the extent of the lens. On the short radius, the lightwood of the outer, sharp, complete, entire growth layer is reduced to a width of one cell which is narrow itself when compared with the lightwood cells at the start of 1936. These features combined with weakness of the densewood make it difficult to resolve the growth layers except under high power. Under low powers, especially, the definition of a growth layer may depend more upon the characteristics of the growth layer succeeding it than it does upon its own characteristics.

1936, at 107 cm.—The two growth layers designated mostly sharp, complete, and entire are thin and lie at the start of the annual increment. At the outside of the chief growth layer there is a 200° sharp, thick, heavily lignified lens. At 89 cm.—On the long radius the inner sharp, complete, entire growth layer has a compound lens of two members; the next outer sharp, complete, entire growth layer likewise has a compound lens; and the third sharp, complete, entire growth layer has a long interior lens. All together, the increment of 1936 at 89 cm. has five lenses arranged radially. Close examination shows that the interior lens actually possesses densewood which is entire around the circuit. The fifth lens lies on the long radius at the outside of the increment.

1937, at 107 cm.—Considerable detail will be given to illustrate the complexity of an annual increment. The 1937 increment consists essentially of two entire growth layers of highly variable relative thicknesses. The inner growth layer has a huge bulge on one radius whereas the outer has one on a different radius. In the bulge of the inner growth layer, there are two sharp exterior half-lenses which face each other and whose densewoods are continuous as a diffuse band. At the bulge of the outer entire growth layer, the great thickness is made up of a sharp lens which contains within it a sharp half-lens, divided densewood, and a sharp overlapping lens in addition to various bands of densewood. The 1937 increment at 89 cm. possesses complexity equal to that at 107 cm. Here the transgressive, or overlapping, lens is in the inner group of growth layers.

At 92 cm. in XSC 1-5 (table 103) five of the lenses are compound, that is, radially placed, and two are concurrent. Both 1938 and 1940 increments at 92 cm. appear to be represented by lenses. However, it is highly probable that only the lightwoods are lenticular. Longitudinal variations in the constitution of the annual increments are only too apparent in XSC 1-5.

A preliminary study of lightwood, densewood bands, and compression-wood zones reveals many detailed alternations of rows of narrow and wide cells. It appears highly reasonable that these inconspicuous alternations, together with the more gross forms of growth layers, record a marked sensitivity to fluctuating physiological conditions. This refers not to random irregularity but to an alignment of cells in a tangential direction.

TABLE 103.—XSC 1-5

	92 cm.	53 cm.
1936	1 sce 1 msce 2 psL	2 sce 1 msce 1 dce
1937	1 sce 1 sL	1 msce 2 ddw
1938	2 sL 1 s $\frac{1}{2}$ L	1 msce 1 msL
1939	1 msce 1 sL ddw	1 sce
1940	4 sL 1 psL 1 dL	1 sce

TABLE 104.—XSC 2-1

	66 cm.	51 cm.
1934-1935	7 sce 2 sL 2 ddw	7 sce 2 sL 2 ddw
1936	1 sce 7 sL	1 sce 7 sL
1937	3 sce 2 sL	3 sce 2 sL
1938	1 sce	1 sce
1939	1 sce 2 sL	1 sce 2 sL 1 msL
1940	inc	inc

The branch XSC 2-1 (table 104) was frozen artificially on April 8, 1940, and cut from the tree May 10, 1940. At 66 cm. the two lenses of 1939 are so thin that they might be called widely divided densewood. They expand outward, at 51 cm., into a distinct lens system, which means the lenses thin inward but lose no definition. The mostly sharp lens at 51 cm. is overlapping.

XSC 2-1 gives us a case where the growth layers are equally sharp along the branch and, except for 1939, show striking vertical uniformity.

Branch XSC 2-2 (table 105) was frozen artificially at 79 cm. on April 11, 1940, and was cut from the tree May 26, 1940. The densewood of the outer lens of 1934 at 67 cm. extends completely around the circuit. In 1936 at 67 cm., the outer margins of the sharp, complete, entire growth layers are not as sharp as they are inward on the

branch. In 1938, the sharp lenses at 96 cm. are compound; at 79 cm., the sharp lens is concurrent; and at 67 cm., the lens has become one long growth layer which is almost entire. The sharp lens of 1940 is concurrent.

TABLE 105.—XSC 2-2

	96 cm.	79 cm.	67 cm.
1934	1 sce 1 dL	1 sce 1 msL	1 sce 2 sL
1935	6 sce	6 sce 1 sL	7 sce 1 sL
1936	5 sce 3 sL 1 msL	5 sce 3 sL 1 msL	5 sce 4 sL
1937	2 sce 1 dce	2 sce 1 dce	2 sce 1 dce
1938	1 sce 2 sL	1 sce 1 sL 1 dL	1 sce 1 sL
	arcs		
1939	1 sce 1 sL	1 sce 1 sL	1 sce 1 sL 1 msL
1940	2 sce 1 sL	2 sce inc	2 sce inc

TABLE 106.—XSC 2-3

	74 cm.	57 cm.	38 cm.
1934-1935	6 msce 1 psL	6 msce 1 psL	6 msce 1 psL
1936-1937	6 msce 2 sL	6 msce 2 sL	6 msce 2 sL
1938	1 sce 1 sL ddw	1 sce 1 sL ddw	1 sce 1 sL ddw
1939	1 sce 1 sL ddw	1 sce 1 sL ddw	1 sce 1 sL ddw
1940	1 sce 1 sL	2 sce	2 sce

Branch XSC 2-3 (table 106) was cut from the tree April 11, 1940, but had not been frozen artificially. Because of the absence of natural frost effects in 1935 and 1937, the annual increments for 1934-1935 and 1936-1937 could not be differentiated. The lenses of 1938 and

1939 are exterior, and the densewoods interior to the lenses are divided, showing that, locally, the cambium and the maturation processes experience multiple rhythmic activity within single growing seasons. Although the number of growth layers in 1940 appears rather excessive in view of the cutting date, a relatively few cells represent each growth layer radially. All our observations and experiments indicate the rapid formation of xylem early in the season. Nevertheless, it would be quite worthwhile to repeat the experiments and observations in order to verify the amount of xylem formed by a date which appears to be rather early in the season.

TABLE 107.—XSC 3-1

	85 cm.	68 cm.	53 cm.
1936-1937	7 msce	4 msce	8 msce
	1 msL	2 sL	2 sL
		ddw	ddw
1938	1 sce	1 sce	1 sce
	2 sL	1 msce	
		2 psL	1 sL
1939	1 sce	1 sce	1 sce
	1 msL	2 msL	1 sL
	1 psL		1 d arc
1940	2 sce	2 sce	2 sce
	2 sL	1 msL	
	4 dL		1 dL
		ddw	ddw
	inc L	inc	inc

XSC 3-1 (table 107) was frozen artificially at 68 cm. on April 11, 1940, and was cut off May 26, 1940. Dating was based on natural frosts. Even if a frost were sufficiently atypical to confuse dating, multiplicity and abundant growth would be characteristic if 1935 is kept barren of frost effects, as it must be. In 1938 at 85 cm., the sharp lenses are compound; in 1939 at 85 and 68 cm., one set of lenses is compound and the other set overlapping.

Freezing and cutting dates for XSC 3-2 (table 108) coincide with those of XSC 3-1. The lenses of 1936 at 112 and 95 cm. are compound; those of 1937 at 80 cm. are concurrent, some sharp, the rest diffuse. In 1938 the lenses are compound. In 1939-1940 the mostly sharp lens is concurrent.

XSC 6-1 (table 109) was frozen artificially April 8, 1940, at 118 cm.

TABLE 108.—XSC 3-2

	112 cm.	95 cm.	80 cm.
1936	1 sce 1 sL 1 dL ddw	1 sce 1 sL 1 dL ddw	1 sce 1 dL
1937	1 sce 1 sL 1 d arc	1 sce 1 sL 1 d arc	1 sce L's
1938	1 sce 2 sL	1 sce 2 sL	1 sce 2 sL
1939-1940	1 sce 1 sL 1 msL inc	1 sce 1 sL 1 msL inc	
1939			1 sce 1 dL
1940			inc

TABLE 109.—XSC 6-1

	118 cm.	89 cm.
1936	1 sce 1 sL	1 sce s $\frac{1}{2}$ L's
1937	1 sce 2 sL 1 dL	1 sce 1 dL s $\frac{1}{2}$ L's d $\frac{1}{2}$ L's
1938	1 sce 1 sL 1 msL ddw	1 sce 1 sL 1 psL
1939	1 sce 1 sL 1 dL	1 sce 2 psL
1940	1 sL inc	inc

TABLE 110.—XSC 8-1

	52 cm.	41 cm.
1937	1 sce	1 sce
1938	2 sce 1 gl 2 msce	1 sce 3 msce
1939	1 sce	1 sce
1940	1 sce 4 sL	2 sce 3 sL
1941	inc	inc

and was cut off May 10, 1940. In the 1938 increment, complexity and sharpness increase inward on the branch.

XSC 8-1 (table 110) was frozen artificially at 41 cm. on May 9, 1941, and was cut off immediately. The so-named "growth layer" of 1938 at 52 cm. was caused by the natural frost of April. It seems probable that one of the lenses of 1940 at 52 cm. became an entire growth layer at 41 cm. In this connection, attention should be called again to longitudinal variations; for instance, the uniformity of 1938 in XSC 3-2 and of 1939 in XSC 8-1, and the variation outward, especially of 1939 in XSC 6-1 and of 1940 in XSC 8-1.

TABLE III.—XSC 8-3

	61 cm.	46.5 cm.	33 cm.
1938	1 sce	1 sce 1 dce	1 sce
	2 d arcs ddw	ddw	
1939	1 sce 1 msce	1 msce 1 psce	1 sce 1 psce 1 dce
	1 dL 1 s arc	1 psL	
1940	1 sce	1 sce 1 psce	1 sce 1 psce
	1 sL	1 sL 1 dL	1 sL
	1 s arc 1 d arc		
1941	inc	inc	inc

XSC 8-3 (table 111) was frozen artificially May 9, 1941, at 46.5 cm., and was cut off May 11, 1941. One of the arcs of 1938 at 61 cm. was frost-made. The sharp lens of 1940 becomes concurrent at 33 cm. Outward on the branch from 61 cm. to 46.5 cm. and 33 cm., the differences in ring patterns and sequences are noteworthy. This branch should be compared with XSC 8-4.

XSC 8-4 (table 112) was frozen artificially May 9, 1941, at 50 cm., and was cut off May 13, 1941. The longitudinal uniformity of this branch should be contrasted with the variation along branch XSC 8-3.

XSC 9-2 (table 113) was frozen artificially at 43 cm. May 9, 1941, and was cut off May 30, 1941. The growth of 1941 is up to seven-eighths as thick as that of 1940; the outer half-dozen cells are immature, and of these the outermost are very narrow. Plates 26, 27, and 28, fig. 1, show one form of longitudinal variation in tree XSC 9.

XSC 9-3 (table 114) was frozen artificially May 9, 1941, at 47 cm., and was cut off June 6, 1941. At 60 cm. the lens of 1939 is concurrent with four members, half of them sharp, half diffuse; outward on the branch the lens apparently becomes an entire growth layer. The incomplete lenses of 1941 have the appearance of what has commonly

TABLE 112.—XSC 8-4

	65.5 cm.	50 cm.	37 cm.
1937	1 sce	1 sce	1 sce
1938	1 sce	1 sce	1 sce
	1 msce	1 msce	1 msce
	1 psce	1 psce	1 psce
	1 sL	1 sL	1 sL
1939	1 sce	1 sce	2 sce
	2 sL	2 sL	2 sL
	1 dL	1 dL	1 dL
1940	2 sce	2 sce	2 sce
	1 msce	1 msce	1 msce
	1 s arc	1 s arc	1 s arc
1941	inc	inc	inc

TABLE 113.—XSC 9-2

	55 cm.	43 cm.	30.5 cm.
1939	1 sce	1 sce	1 sce
	1 psce	1 psce	
	2 dce	2 dce	
	1 sL (long)	1 sce	1 dL
1940	1 sce	1 sce	1 sce
	1 msce		
	1 psce	2 psce	3 psce
		1 psce	1 dce
	1 msL		
1941	inc	inc	inc

been called postseasonal growth, a designation difficult to apply here because of the early cutting date.

XSC 9-4 (table 115) was frozen artificially at 46 cm. on May 9, 1941, and cut off June 14, 1941. At 57 cm. the outer sharp, complete, entire growth layer of 1939 is very thin and possesses a thin, weak band of densewood compared with that of the inner growth layer. At 46 cm. the inner growth layer has become indefinite over a portion of its circuit, and the outer one is thinner. The inner growth layer has become totally diffuse at 34 cm. and its densewood joins that of the

outer growth layer making the lightwood of the outer lenticular. In other words, the outer growth layer of 1939, which constitutes the annual boundary, becomes thicker inward on the branch as well as less decisive in its differentiation from enclosing growth layers. The incomplete, entire growth layers of 1941 at 46 and 34 cm. are just as

TABLE 114.—XSC 9-3

	60 cm.	53 cm.	47 cm.	37 cm.
1938	2 sce	2 dce	1 sce 1 dce	1 sce
1939	1 sce 1 dce 1 L (conc. s+d)	1 sce 1 dce 1 psce	1 sce 1 dce 1 psce	1 sce 1 dce 1 dce
1940	2 sce 1 msL (long) 1 sce	1 sce 1 msce 1 psL 1 sL	1 sce 1 psce 1 dL (faint) 1 dL	1 sce 2 psce 1 d arc ddw
1941	1 sce inc L's	1 sce inc L's	1 sce inc L's	1 dce inc

TABLE 115.—XSC 9-4

	57 cm.	46 cm.	34 cm.
1938	1 sce 1 dce 1 L	1 sce 1 dce 1 sL	1 sce (faint)
1939	2 sce ddw	1 sce 1 msce	1 sce 1 dce
1940	3 sce 1 msL	1 sce 2 msce 1 gl ddw	1 sce 1 psce 1 dce ddw
1941	1 sce inc L	inc	inc

thick as at 57 cm., but the outer three to four rows of cells on each are immature. There is no indication of densewood.

XSC 9-5 (table 116) was frozen artificially at 42.5 cm. on May 9, 1941, and was cut off June 20, 1941. In the 1937 increment, the diffuse, complete, entire growth layer at 48.5 cm. is fading rapidly. In 1938 a new diffuse, complete, entire growth layer appears at 42.5 cm., but all of them at 33.5 cm. are faint or entirely gone. The outer sharp,

complete, entire growth layer of 1939 is somewhat obscure because it is thin and because its densewood is a very thin thread. The growth layers of 1939, other than the two sharp, complete, entire growth layers, are becoming highly diffuse and disappearing at 33.5 cm. At 48.5 cm. a diffuse lens barely begins, a lens quite plainly visible out at 42.5 cm. but entirely gone at 33.5 cm.

TABLE 116.—XSC 9-5

	52.5 cm.	48.5 cm.	42.5 cm.	33.5 cm.
1937	1 sce 1 psce	1 sce 1 dce	1 sce	
1938	1 sce 1 psce 1 dce 1 sL	1 sce 2 dce 1 sL	1 sce 3 dce 1 sL	1 sce 3 dce 1 dce
1939	2 sce 1 msL	2 sce 1 msL	2 sce 1 msL 1 dL	2 sce
1940	2 sce 1 sL	2 sce 1 sL	2 sce 2 sL	2 sce 1 sL ddw
1941	1 sce psg	1 pce	inc	inc

Under low power one of the sharp, complete, entire growth layers of 1940 is actually divided densewood which broadens outward on the branch. At 48.5 cm. the short, sharp lens of 52.5 cm. has narrowed down until it is merely divided densewood; at 42.5 cm. a new lens system appears, a compound lens of two members, one of which narrows at 33.5 cm. to divided densewood.

XSC 9-6 (table 117) was frozen artificially May 9, 1941, and was cut off June 27, 1941. In the 1938 increment, the mostly sharp, complete, entire growth layer and the diffuse, complete, entire growth layer become more diffuse outward from 46 cm., so much so that they have practically disappeared at 29 cm. In 1939 the diffuse lens weakens outward to faintness at 40 and 29 cm. In 1940 one of the sharp, complete, entire growth layers at 52 cm. is sufficiently narrow to be classed perhaps as divided densewood. At 46, 40, and 29 cm. it is the diffuse portion of the mostly sharp, complete, entire growth layer which has the divided densewood. The two sharp lenses are equivalent to one compound lens whose borders become slightly less definite outward.

XSC 10-1 (table 118) was frozen artificially at 34.5 cm. on May 9,

1941, and was cut off July 4, 1941. In the 1939 increment, the intra-annuals fade outward. In 1940 the arc was made by natural spring frost. In 1941 the lenses are concurrent.

XSC 10-3 (table 119) was frozen artificially at 36 cm. on May 9, 1941, and was cut off July 22, 1941. In the 1939 increment, complexity decreases outward.

TABLE 117.—XSC 9-6

	52 cm.	46 cm.	40 cm.	29 cm.
1938	1 sce 2 msce 2 psce 1 s arc	2 sce 1 msce 1 dce	2 sce 2 dce	1 sce
1939	1 sce 1 msce 1 dL	1 sce 1 msce 1 dL	1 sce 1 dce 1 dL	1 sce 1 dce 1 dL
1940	2 sce 2 sL	1 sce 1 msce ddw 2 sL	1 sce 1 msce ddw 2 sL	1 sce 1 msce ddw 2 sL
1941	1 sce psg	1 sce	1 sce	1 pce

XSC 11-2 (table 120) was frozen artificially at 38 cm. on May 9, 1941, and was cut off September 11, 1941. In the 1938 increment, the lens is concurrent in each case and becomes thicker outward. In 1939 the densewood at 44 cm. resulted from frost action. As is so common in 1939, the outer entire growth layer is very thin and weak, its densewood one to two rows of cells thick. Here and there radial columns of cells fail to narrow down, thus creating "gaps" in the densewood. It should be noted that all these so-called outer thin growth layers, weak and inconspicuous though they may be, constitute the outer portions of the annual increments. In many cases the inner growth layer, or intra-annual, is more distinct, more conspicuous, and more developed.

XSC 11-3 (table 121) was frozen artificially at 38 cm. on May 9, 1941, and was cut off September 27, 1941. In the 1938 increment, one of the sharp growth layers was caused by the 1938 natural frost with which it is connected. At 38 cm. the only visible frost effects are a circle of parenchyma cells and the band of densewood. The densewood of the annual increment is divided over a major portion of its circuit. At 29 cm. the divided densewood has actually become a genuine, complete, entire growth layer. Within incipient compression

TABLE 118.—XSC 10-1

	45.5 cm.	40.5 cm.	34.5 cm.	23 cm.
1939	1 sce 1 psce 1 dce	1 sce 2 dce	1 sce 1 dce ddw	1 sce
1940	2 sce	1 sce 1 msce	1 sce 1 psce	1 sce ddw 1 arc
1941	1 sce inc L's	1 sce inc L's	inc	inc

TABLE 119.—XSC 10-3

	51 cm.	42 cm.	36 cm.	24 cm.
1939	1 sce 1 msce 1 psL 1 dL	1 sce 1 dce	1 sce 1 dce	1 sce
1940	1 sce 1 dL ddw	2 dL 1 sce 1 dL 1 psL	1 sce 1 sL 1 psL	1 psce 1 sce 1 sL 1 psL
1941	1 sce 1 d arc psg	inc	inc	inc

TABLE 120.—XSC 11-2

	49 cm.	44 cm.	38 cm.	26 cm.
1938	1 sce 1 dce 1 dL ddw	1 sce 1 dce 1 psL	1 sce 1 dce 1 psL	1 sce 1 dce
1939	1 msce 1 psce 1 dL 1 d $\frac{1}{2}$ L	1 msce 1 psce 1 dL 1 d $\frac{1}{2}$ L dw	1 msce 1 psce 1 dL 1 d $\frac{1}{2}$ L	1 sce 1 psce 2 dL 1 d $\frac{1}{2}$ L
1940	1 sce 1 psce 1 sL	1 sce 1 psce 1 sL	1 sce 1 psce 2 sL	1 sce 1 psce 2 sL
1941	1 sce psg	inc	inc	inc

wood, thin zones of slightly narrower cells form a rhythmic pattern. In 1939 of XSC 11-3, in contrast with XSC 10, the outer growth layer is thicker and cannot be called an "outer thin" growth layer. The densewood of this outer growth layer becomes threadlike outward at 44 cm. The densewood band of the partly sharp, complete, entire growth layer at 38 cm. is replaced outward at 29 cm. by three bands

TABLE 121.—XSC 11-3

	47 cm.	44 cm.	38 cm.	29 cm.
1938	2 sce ddw	2 sce ddw	2 sce ddw	2 sce 1 dce
1939	1 sce 1 msce	1 sce 1 psce 1 psL	1 sce 1 psce	1 sce 3 dce
1940	1 sce 1 sL 1 msL	1 sce 1 sL 1 msL	1 sce 1 sL 1 msL	1 sce 1 sL
1941	1 sce psg	inc	inc	inc

TABLE 122.—XSC 12-1

	52 cm.	48 cm.	42 cm.	33 cm.
1938	3 sce 1 dL dw	3 sce 1 dL	1 sce	1 sce
1939	2 sce 1 dL ddw	2 sce 1 dL ddw	2 sce 1 dL 1 sL	2 sce 1 dL 1 sL
1940	1 sce 1 msce 1 sL 1 d $\frac{1}{2}$ L	1 sce 1 msce 1 sL 1 d $\frac{1}{2}$ L	1 sce 1 psce 1 msL 1 d $\frac{1}{2}$ L	1 sce 1 dce 1 psL 1 d $\frac{1}{2}$ L
1941	1 sce psg	inc	inc	inc

of diffuse densewood. In 1940 the sharp lenses are compound. The mostly sharp lens is a concurrent system of two lenses, one of which is sharp and the other diffuse-margined. On the whole, the two branches of XSC 11 possess a relatively high degree of continuity along their lengths.

XSC 12-1 (table 122) was frozen artificially at 42 cm. on May 9, 1941, and was cut off October 11, 1941. In the 1938 increment, the three sharp, complete, entire growth layers at 48 cm. are weaker than

they are inward on the branch; at 42 cm. two of them are so dim as to be unrecorded in analysis; at 52 cm. the lightwood of the outer growth layer disappears on one radius. The densewood (dw) at 52 cm. is connected with natural frost injury. Tree XSC 12 shows the "outer thin" growth layer of 1939 in striking fashion. The divided densewood becomes a sharp lens outward. In the 1940 increment, all intra-annuals become progressively weaker and more diffuse outward on the branch.

TABLE 123.—XSC 12-2

	62 cm.	57 cm.	51 cm.	42 cm.
1938	1 sce 1 msce	1 sce 1 msce	1 sce 1 msce	1 sce
				2 dce
	1 psce 2 sL	1 psce 2 sL	1 psce 2 sL	2 msL ddw
1939	2 sce 1 dL ddw arcs	2 sce 1 dL ddw arcs	2 sce 1 dL ddw arcs	2 sce 1 dL
1940	2 sce 1 sL ddw	2 sce 1 sL ddw	2 sce 1 sL ddw	2 sce 1 sL ddw
1941	1 sce psg	inc	inc	inc

XSC 12-2 (table 123) was frozen artificially at 51 cm. on May 9, 1941, and was cut off December 6, 1941. In the 1938 increment, the sharp lenses are compound, centering on the same radius inward on the branch but "sliding off" each other outward. The divided densewood affects the densewood of the outer lens. In the 1939 increment, the arcs refer to partial bands of densewood scattered throughout the lightwood. In the 1940 increment, the sharp lenses are concurrent.

XSC 13-1 (table 124) was frozen artificially at 38 cm. on June 14, 1941, and was cut off June 20, 1941. In the 1938 increment at 50.5 cm., the sharp lens and the divided densewood are one continuous growth layer at the outer margin of the annual increment. They are gone at 38 cm. Although the narrowing of 1938 outward at 27 cm. accounts for the disappearance of some of the intra-annuals, it does not account for the disappearance of all of them. The "outer thin" growth layer of 1939 is striking in tree XSC 13. For a long distance around the circuit, at 38 cm., the densewood of the annual increment

contains only one narrow densewood cell radially. Multiplicity in 1938 decreases outward, whereas in 1940 it increases outward.

The impact of artificial freezing on the formation of xylem emphasizes the variations brought about by different conditions in different years, on different sections, and even on different branches. Ex-

TABLE 124.—XSC 13-1

	50.5 cm.	38 cm.	27 cm.
1938	3 msce 1 psce 1 sL ddw	2 sce	1 sce
1939	3 sce 1 dce	3 sce 1 dce 1 msL ddw	3 sce 1 msL
1940	1 sce ddw	1 sce 1 msL 1 dL ddw	1 sce 1 msL 1 dL
1941	inc	inc	inc

TABLE 125.—XSC 13-2

	46.5 cm.	40 cm.	40—cm.	34 cm.	27 cm.
1938	1 sce 1 msce 1 s arc	1 sce 1 msce 1 dL 1 s arc	1 sce 1 psce 1 dL 1 s arc	1 sce 1 dce 1 dL 1 d arc	1 sce 1 dce 1 dL 1 d arc
1939	2 sce 1 sL 1 dL	2 sce 1 sL 2 dL	2 sce 2 sL 1 dL	2 sce 2 sL 1 dL	2 sce 2 sL 1 dL
1940	1 sce 1 s $\frac{1}{2}$ L 1 d $\frac{1}{2}$ L	1 sce 1 s $\frac{1}{2}$ L 1 d $\frac{1}{2}$ L	1 sce 1 s $\frac{1}{2}$ L 1 d $\frac{1}{2}$ L	1 sce 1 s $\frac{1}{2}$ L 1 d $\frac{1}{2}$ L	1 sce 1 s $\frac{1}{2}$ L 1 d $\frac{1}{2}$ L
1941	1 pce psg	1 ce psg	1 pce psg	1 pce psg	1 pce psg

tensive application of artificial freezing would no doubt yield much information on the exact time of xylem deposition under various conditions.

XSC 13-2 (table 125) was frozen artificially at 34 cm. on June 14, 1941, and was cut of June 27, 1941. In the 1938 increment, all intra-annuals become weaker and progressively more diffuse outward on the branch. The sharp portions of the mostly sharp, complete, entire

growth layer and arc at 46.5 cm. overlap, so that where one is sharp the other is diffuse radially from it. Because this is not true outward, the sharp margin of one or the other must spiral outward. In 1939 the "outer thin" growth layer at 40 cm. expands on the long radius into a thickness two and one-half times that of the inner growth layer and acquires a diffuse lens which, within a relatively few microns (at 40— cm.), becomes sharp bordered. Branch XSC 13-2 possesses much more uniformity throughout its length than does branch XSC 13-1.

TABLE 126.—XSC 13-3

	44 cm.	42 cm.	33 cm.	28 cm.
1937	1 sce 1 dce	1 sce 1 dce	1 sce	1 sce
1938	1 sce 1 sL 1 msL	1 sce 1 sce 1 msce	1 sce 1 sL 1 msL	1 sce 1 sL 1 msL
1939	1 sce 1 sL	1 sce 1 sL	1 sce 2 sL	1 sce 1 sL
1940	1 sL	1 sL	1 sL	1 sL
1941	1 sce psg	1 sL psg	1 spce psg	1 sce psg

TABLE 127.—XSJf 1-1

	65 cm.	50 cm.	36 cm.
1937	1 sce	1 sce	1 sce
1938	1 sce 1 dce ddw	1 sce 1 dce ddw	1 sce 1 dce
1939	1 sce 1 sL	1 sce 1 dL	1 sce 1 dL
1940	inc	inc	inc

XSC 13-3 (table 126) was frozen artificially at 33 cm. on June 14, 1941, and was cut off July 11, 1941. In the 1938 increment, the sharp lenses at 44, 33, and 28 cm. and the sharp, complete, entire growth layer at 42 cm. are connected with, and very probably induced by, the 1938 natural frost. In the 1939 increment at 33 cm., the two sharp lenses are one compound lens. In the 1940 increment, the table seems to indicate that here we have a case where a lens—a partial growth layer—represents all the growth for an entire growing season. However, it is highly probable that the densewood encircles the sections.

XSJf 1-1 (table 127) was frozen artificially at 50 cm. on May 10,

1940, and cut off June 12, 1940. In the 1938 increment, the diffuse growth layer fades outward. In the 1939 increment, the sharp lens of 65 cm. becomes diffuse at 50 cm. but sharpens on several radii at 36 cm. The densewood of the annual border at 50 cm. weakens so much that it appears to be diffuse when viewed under low power.

TABLE 128.—*XSJf 2-1*

	61 cm.	50 cm.	36 cm.
1937	I sce arcs	I sce arcs	I sce arcs
1938	I sce I dce	I sce I dce	I sce I dce
1939	I sce I dce	I sce I dce	I sce I dce
1940	I sce ddw inc	I sce ddw inc L's	I sce ddw inc

XSJf 2-1 (table 128) was frozen artificially at 50 cm. on May 10, 1940, and was cut off June 12, 1940. The compression wood of 1937 carries numerous arcs of narrow cells. In the 1938 and 1939 increments, the diffuse intra-annuals become more diffuse and fainter outward on the branch. The sharpness of the divided densewood at 61 cm. of 1940 fades outward.

TABLE 129.—*XSP 1-1*

	49 cm.	33 cm.	19 cm.
1937	I sce	I sce	I sce
1938	I sce I sL	I sce ddw	I sce
1939	I sce	I sce	I sce
1940	I sL inc L	I sce I sL inc	inc

XSP 1-1 (table 129) was frozen artificially at 33 cm. on May 10, 1940, and was cut off June 12, 1940. In the 1938 increment, the sharp lens at 49 cm. is reduced to divided densewood at 33 cm. and has disappeared before reaching 19 cm. The sharp, complete, entire growth layer of 1940 at 33 cm. actually possesses lenticular lightwood.

XSP 1-2 (table 130) was cut off February 22, 1941. The "complete entire" growth layer of 1940 has weak, intermittent densewood. At the gaps, the cells give no indication of narrowing as is to be expected in the development of normal densewood. Although the annual increments in the Experiment Station pines possess multiplicity, it is not so great as in the Arizona cypresses.

TABLE 130.—XSP 1-2

	45 cm.	16 cm.	TF
1937	1 sce		
1938	1 sce ddw		
1939	1 sce	1 sce	1
1940	2 sce 1 sL 1 ce	2 sce 1 sL 1 ce	2

TABLE 131.—XSP 2-1

	42 cm.	32 cm.	20.5 cm.
1936	2 sce 1 dL	1 sce	
1937	1 sce arcs	1 sce	1 sce
1938	2 sce ddw	2 sce 2 dL	2 sce
1939	1 sce 1 dL	1 sce 1 sL	1 sce 1 sce
1940	inc	inc	1 sL inc

TABLE 132.—YCt 1-4

	12 cm.	5.5 cm.	TF
1940	2 sce	1 sce	1

XSP 2-1 (table 131) was frozen artificially at 32 cm. on May 10, 1940, and was cut off June 12, 1940. In the 1937 increment, the arcs are of densewood confined to the long radius.

Branch YCt 1-4 (table 132) came from a single tip flush which represented the entire growth for 1940.

Branch YCt 1-5 (table 133) possessed two tip flushes for the growth of 1940. Sections at 15 cm. came from the inner, and those at 12 cm.

came from the outer, tip flush. Growth was taking place when the branch was cut from the tree.

Branch YCt 1-6 (table 134) possessed two tip flushes for 1940. Sections at 16.5 cm. came from the inner, and those at 13.5 cm. came from the outer, tip flush.

TABLE 133.—YCt 1-5

	15 cm.	12 cm.	TF
1940	2 sce	1 sce	2
	1 L (?)		
	1 gl (?)	1 gl (?)	

TABLE 134.—YCt 1-6

	16.5 cm.	13.5 cm.	TF
1940	3 sce	1 sce	2

TABLE 135.—YCt 2-2

	24 cm.	7 cm.	TF
1939-1940	3 sce	3 sce	2 (p)
	5-6 sL	3 sL	
	psg	psg	

TABLE 136.—YCt 2-3

	19 cm.	5 cm.	TF
1939-1940	8-10 sce	8- sce	2 (p)
	sL's	sL's	
	psg	psg	

TABLE 137.—YCt 2-5

	32 cm.	19.5 cm.	14 cm.	8.5 cm.	4 cm.	TF
1939-1940	6 sce	8 sce	10+ sce	10++ sce	5 sce	5 or
	6 L	L's	L's	L's	1-2 L	5 +
	psg	psg	psg	psg	inc L	

The measurements at the head of the table for YCt 2-2 (table 135) are distances inward from the outer end of 1939 tip growth. This holds for the remainder of the YCt's. All of them were cut from the trees November 26, 1940, and were growing at the time.

Branch YCt 2-3 (table 136) contained only the growth for 1939-1940. A great disparity exists between the number of tip flushes and the number of diameter flushes.

The sections at 32 cm. of YCt 2-5 (table 137) were taken from the

first tip flush of 1939, and those at 4 cm. were taken from the fifth or outer tip flush.

TABLE 138.—*YCt 3-1*

	9.5 cm.
1938-1940	11-13 sce L's psg

TABLE 139.—*YCt 3-2*

	6 cm.
1938-1940	11+ sce L's psg

The sections of *YCt 3-1* (table 138) were taken 9.5 cm. inward from the outer end of 1938 tip flush.

The sections of *YCt 3-2* (table 139) were taken 6 cm. inward from the outer end of 1938 tip flush. Some of the lenses are compound. Branches *YCt 3-1* and *3-2* possess remarkable multiplicity, a multiplicity which is not too surprising in the environment of the Experiment Station at Yuma, Ariz.

TABLE 140.—*YCt 4-1*

	12 cm.
1937-1940	16 sce L's psg

The sections of *YCt 4-1* (table 140) were cut 12 cm. inward from the outer end of 1937 tip flush. Diameter growth was proceeding rapidly when the branch was cut off November 26, 1940.

TABLE 141.—*YCt 4-2*

	8 cm.
1937	3 sce 1-2 L
1938	2 sce
1939	2 sce 2-4 L
1940	5 sce L's psg

Annual increments in *YCt 4-2* (table 141) were tentatively distinguished on a color basis; there is no assurance of accuracy. Growth over a period of four years included 12 sharp, complete, entire growth layers and an additional number of lenses.

Longitudinal variations, present in branches, are amply illustrated by the foregoing tables and discussions. On the whole, the variations are neither so numerous nor so striking as they are among different radii of the same section. At least a person is left with such an impression, probably because the composite picture of one section is compared with the composite of another.

A study of sections as individuals and as parts of branches illustrates clearly the transition of one growth-layer type into another, the need for a classification of growth layers, and the basis of a classification as a descriptive localization in time and in space.

Both circuit and longitudinal variation are high among the branches of trees grown under lower forest-border conditions. With increase in altitude, that is, with increase in rainfall and with decrease in amplitude or rainfall fluctuations, variations of growth layers around and along branches decrease. Simplicity of classification increases.

No general rule of longitudinal variation emerges from a study of many branches from many trees. The amount of variation, or multiplicity, along a branch may remain the same, or it may increase inward or outward on the branch. On a single branch one annual increment may increase in multiplicity outward, whereas another annual increment may increase in the opposite direction. A rough census of the behavior of the annual increments in the different branches showed nearly double the number of cases where multiplicity decreased outward over the number which remained the same or increased.

RELATION OF DIAMETER FLUSHES TO TIP FLUSHES

The relationship between diameter flushes and tip flushes is closely connected to the longitudinal habit of growth layers in a single branch. Ordinarily, of course, one tip flush is thought to represent one growing season. Actually, tip flushes may be dual, or even multiple, and their relations to diameter flushes rather complex.

No question arises as to the identity of a second tip flush if tip growth has been measured accurately or closely observed day by day. In such case, the presence of terminal bud scale scars between the two flushes of the same season corroborates the evidence of the measurements. The second tip flush is commonly much shorter than the first, but this fact cannot be used alone as evidence of two flushes. Indeed, on occasion, the first flush is the shorter, e.g., 1942 of Con T 2-6, 0.8 cm. and 2.8 cm.; of Con T 2-7, 0.9 cm. and 3.3 cm.; and of Con T 2-8, 0.3 cm. and 1.6 cm. In the same set of branches, Con T 2-5 showed 2.8 cm. and Con T 2-4 showed 2.0 cm. in a single flush for

1942. In contrast, two tip flushes may be of unequal length as in Con T 2 where they were 11.5 cm. and 2.3 cm., or they may be of approximately the same length as seen in Con T 1-11 to 1-14. One branch of a peach tree (WPe 1-4), at the border of the District of Columbia in Maryland, set three successive terminal buds before it ceased growth for the season of 1944. The three tip flushes were, in an outward direction, 12.5, 14.0, and 11.5 cm. long.

The matter goes farther. Terminal bud scale scars represent a final step in the transition from growth slowdown to cessation of tip elongation. Before the final stage, there are all degrees of slowdown from continuous growth to complete cessation one or more times during a single season. With angiosperms, the evidence rests not only upon periodic measurement and close observation but also upon the lessened distance between leaf scars. With gymnosperms, especially the pines, the evidence rests not upon leaf scars but upon a succession of bare-needle zones. Details will be given later in this section.

Correspondence of diameter flushes with tip flushes.—No mention would be necessary if this were a one-to-one relationship. The following is a list of possible correspondence with a minimum of complexity:

1. One diameter flush to one tip flush.
2. One diameter flush to two tip flushes.
3. Two diameter flushes to one tip flush.
4. Two diameter flushes to two tip flushes.
5. Multiple diameter flushes to multiple tip flushes.

A few examples of each type are given below.

1. Of this type, illustrations have been detailed previously. It is, no doubt, the most prevalent.

2. In consideration of the apparently high incidence of multiple tip flushes under certain climates, one is surprised to learn, from all the materials at hand, that single diameter flushes for multiple tip flushes occur more rarely than multiple diameter flushes for single tip flushes.

Con T 1-1	1939: 1 df—3 tfs
Con T 1-6	1940: 1 df—2 tfs
Con T 2-4	1941: 1 df—2 tfs
Con T 2-8	1941: 1 df—2 tfs
	1942: 1 df—2 tfs
MP 1-2	1941: 1 df+d arcs—2 tfs
TTP 23-9	1943: 1 df—2 tfs
TTP 24-8	1945: 1 df—2 tfs
	1945: 1 df—2 tfs
TTP 24-20	1941: 1 df—2 tfs
	1942: 1 df—2 tfs

It is unknown whether or not, under MP 1-2 above, the arcs correspond to the inner of the two tip flushes. The two entries under TTP 24-8 above apply to two different side branches.

3. Two diameter flushes correspond to one tip flush.

Con P 2-2-b	1944:	2 dfs + ddw—I tf
Con T 1-10	1941 (2nd):	4 + dfs—I tf
Con T 2-2	1940:	3 dfs—I tf
TRA 1-1	1942:	inc—no tf
TRP 1-1	1942:	inc—no tf
TTAp 1-2-a	1939:	2 dfs—I tf
TTAp 1-4-a	1939:	1 df + 1 s arc—I tf
TTAp 2-1-a	1938:	2 dfs—I tf
	1939:	2 dfs—I tf
TTAp 2-2-a	1939:	2 dfs + arcs + $\frac{1}{2}$ L's—I tf
TTM 2-5-a	1941:	2 dfs—I tf
TTP 20-16	1943:	2 dfs—I tf
	1944:	3 dfs—I tf
TTP 20-20	1942:	2 dfs—I tf
TTP 20-23	1944:	3 dfs—I tf
TTP 23-9	1944:	2 dfs—I tf
TTS 1-1	1937:	3 dfs + arcs—I tf
YCt 1-3	1940:	4 dfs—I tf

Attention should be directed to TRA 1-1 and TRP 1-1, representing two different genera, which had produced no tip growth by June 28, but which had made diameter growth. In TRA 1-1, 1942 xylem was an incomplete, but entire, growth layer. In TRP 1-1-a, 1942 xylem consisted of several short lenses up to three cells thick; in 1-1-b, 1942 was a single 100° lens two cells thick; in sections *c*, 1942 was one lens of 45° two cells thick; and in sections *d*, 1942 consisted of two to four cells around the entire circuit. Amount of xylem neither increased nor decreased uniformly along the branch.

4. Two diameter flushes correspond to two tip flushes per year.

Con T 1-5	1942
Con T 1-6	1941
Con T 1-11	1940
Con T 1-12	1940
Con T 1-18	1942: 1 df + psg—2 tfs
Con T 2-3-a	1938: 1 df + 1 d arc—2 tfs
	1939: 1 df + 1 d arc—2 tfs
Con T 2-6	1942
TTAp 1-2-a	1938
TTAp 2-2-a	1938
TTAp 2-3-a	1938
TTP 20-16	1942
TTP 20-25	1944
TTP 20-27	1943

TTP 20-33	1943
WAp 1-3	1944
WCh 2-3	1944
WPc 1-2	1944

5. Multiple diameter flushes correspond to multiple tip flushes.

Con T 2-2-a	1938-39:	4 to 5 dfs—3 tfs
Con T 2-3-c	1939:	3 dfs—2 tfs
LVP 1-2	1935 (?) -40:	6 dfs—5 tfs
TRA 1-1	1934 (?) -41:	8 dfs—7 tfs
TRAsp 1-1-a	1930 (?) -40:	11 dfs—8 tfs
TTAp 1-4-a	1938:	3 dfs—2 tfs
TTAp 2-3-a	1939:	5 dfs + 1 d $\frac{1}{2}$ L—2 tfs
TTM 1-1-a	1935 (?) -40:	8 dfs—6 tfs
TTP 20-4	1936-39:	11 dfs—5 tfs
TTP 20-13	1940-41:	4 dfs—2 tfs
TTP 21-1	1935-39:	7 dfs—6 tfs
TTP 21-2	1937-40:	8 dfs + arcs—5 tfs
TTP 21-7	1935-40:	8 dfs—5 tfs
TTP 21-10	1936-41:	8 dfs—9 tfs
TTP 22-2	1940-41:	4 dfs—2 tfs
TTP 24-10	1938-42:	8 dfs—5 tfs
WCh 2-6	1944:	3 dfs—2 tfs
WPc 1-4	1944:	2 dfs—3 tfs
YCt 1-6	1940:	3 dfs—2 tfs

Insofar as our materials are concerned, the one-to-one correspondence, number 1, is the most common and number 5, the second. The preponderance of unity or of multiplicity depends to a certain extent, apparently, upon the rainfall, and hence the soil-moisture regime under which the respective trees grew.

*The problem of growth slow-down.*⁷—The presence of terminal bud scale scars leaves no doubt that tip growth ceased at least temporarily during a particular growing season. But that they always occur at the end of a year, or that diameter growth ceases with tip growth, is not necessarily true.

The condition of continuous growth throughout a season gives way gradually to a situation wherein, by successive stages, growth slows down increasingly until the final stage of complete cessation, once or more within the season. In gymnosperms, the problem intermediate between the two extremes resolves itself into a study of sets of so-called bare-needle zones. In angiosperms, it is a study of shortened intervals between leaves or their scars.

⁷ Because of continued repetition of descriptive phrases in this section, they are abbreviated as listed on page 101.

The inner portion of a bare-needle zone bears no needles whereas the outer portion does. One ordinarily assumes that a bare-needle zone constitutes a tip flush, set off inward and outward by terminal bud scale scars. This, however, does not always follow because two sets of bare-needle zones between terminal bud scale scars are rather common.

TTP 20-15 was observed almost daily and was measured weekly from October 11, 1941, to December 31, 1942. By April 4, 1942, the terminal bud had increased in length to 4.0 cm.; by April 11 the new growth had lengthened to 4.3 cm.; and by April 19 to 6.3 cm., which, excluding the terminal bud, comprised the season's tip growth. Little growth was noted between April 4 and 11 whereas a 50-percent increase in length occurred between April 11 and 19. This great increase formed the second set of bare-needle zones for the season. The diagram, text figure 42, shows the relationship when the branch was cut

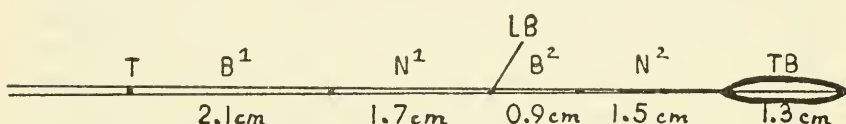


FIG. 42.—Tip growth for 1942 on TTP 20-15. T, terminal bud scale scars at end of 1941. B¹ and B², bare spaces; N¹ and N², spaces bearing needles. TB, terminal bud; and LB, lateral bud.

off December 31, 1942. No terminal bud scale scars separate N¹ and B²; however, B² had a slightly constricted appearance, especially at the start, and could easily be mistaken for the beginning of a year's growth. In spite of appearances, the growth for 1942 contains but one tip flush.

Cross sections in TTP 20-15 were taken from 1941 growth, from zone B¹ (text fig. 42), from zone N¹, and from N². The two sections from 1941 and those from B¹ and N¹ showed 1 sce for 1942. Scattered narrow cells within the body of the 1942 increment could in no sense be interpreted as continuous. It is not surprising to find a lack of distinction in the xylem between a bare zone and its following needle zone, but it is somewhat surprising that the two sets of bare-needle zones are not distinct in the xylem. This could mean, of course, that tip growth did cease for a very brief time, so brief, in fact, that densewood failed to form in the xylem.

In contrast with the preceding, TTP 20-20 was cut from the tree on April 25, 1942, by which time two sets of bare-needle zones had been formed, the first 6.7 cm. long and the second 3.3 cm. No terminal bud scale scars separated the two sets. Sections *a* from the inner bare zone

contain one incomplete, entire growth layer plus a zone of narrow cells in the form of a broken circle—the merest hint of an intra-annual. In sections *b*, from the inner needle zone, the diffuse broken growth layer is a trifle more definite. Sections *c* and *d*, from the outer bare and outer needle zones respectively, contain only incomplete lenses for 1942. There is here, then, some evidence of a fluctuation in the rate of diameter growth to correspond with a like variation in the rate of tip growth. The broken thin band of narrow cells in sections *a* occurs about five to seven cells inward from the cambium in the as yet immature xylem. Of course, it might well be that a definite entire band of narrow cells is not in existence because of immaturity and that such a zone might have been present had the 1942 growth been permitted to go to maturity.

The sections from TTP 20-21 were cut off the tree May 7, 1942. At the time of cutting, 1942 tip growth contained two sets of bare-needle zones not separated from each other by terminal bud scale scars. The inner set measured 9 cm. and the outer set measured 3 cm. The terminal bud was 0.8 cm. long. Three pistillate cones arose from the base of the outer bare zone. Sections *a* from the inner bare zone contain 1 sce and one incomplete, entire growth layer. The 1 sce makes up three-fourths of the total xylem, thus comparing favorably with the proportions between the two sets of bare-needle zones in the tip growth. Sections *b* from halfway out in the inner needle zone contain one incomplete, entire growth layer. Farther out the branch, the sections from the second set of bare-needle zones contain an incomplete lens each. Insofar as sections *a* are concerned, TTP 20-21 gives a clear-cut example of two growth layers for two sets of bare-needle zones, and there would be no hesitation in correlating the two. Sections *b*, however, do not show the extra growth layer, and its absence can only mean that a growth layer to match a tip flush is present inward on the branch but absent outward. It may well be that a tree makes a special effort to keep vital processes continuous near the growing tips.

TTP 20-21 with two growth layers suggests that TTP 20-20 with a hint of an extra growth layer is a transition between TTP 20-15 with 1 sce and TTP 20-21 with 2 sce. Apparently the presence of a lateral bud between the two sets of bare-needle zones of TTP 20-15, the three pistillate cones of TTP 20-21, and neither in TTP 20-20 gives evidence that they have no significance as markers, either of a second tip flush or of a second diameter flush.

The 1941 tip growth of TTP 24-9 contained two sets of bare-needle

zones, the inner of 8.8 cm. and the outer of 3.5 cm. No terminal bud scale scars and no lateral buds marked the separation between the two sets. A section taken from the inner needle zone contains 1 sce only.

TTP 24-12 comprised the inner part and TTP 24-23 the outer part of a single branch cut off January 1, 1943. In the tip growth for 1941, the inner set of bare-needle zones measured 5.4 cm. and the outer 3 cm. In the tip growth for 1942, the inner set measured 6.3 cm. and the outer 3 cm. Terminal bud scale scars separated the two annual flushes whereas a small branch emerged from the base of the outer bare zone of 1941, and pistillate cones emerged from the like place of 1942. In 1942, total tip growth had been essentially completed by May 16.

Sections *a*, TTP 24-12, 53.5 cm. from tip of terminal bud, in 1937 tip flush, show 1 sce each for 1941 and 1942.

Sections *b*, 40 cm. from tip, in 1938 tip flush, show 1 sce for 1941 and 1 sce plus 1 psce for 1942. In fact, the psce actually grades into ddw on one arc.

Sections *c*, 30.5 cm. from tip, in 1939 tip flush, show 1 sce for 1941 and 1 sce plus 1 dce for 1942.

Therefore, 1941 contains one growth layer for two sets of bare-needle zones whereas 1942 contains two growth layers for two sets.

Sections *a* of TTP 24-23, 15.2 cm. from base of terminal bud, in inner needle zone of 1941, contain 1 sce for 1941 and 1 sce for 1942.

Sections *b*, 10.8 cm. from base of terminal bud, in outer needle zone of 1941, contain 1 sce for 1941 and 1 sce plus psg for 1942.

Sections *c*, 4.4 cm. from base of terminal bud, in inner needle zone of 1942, contain 1 sce plus psg.

Sections *d*, 1.5 cm. from base of terminal bud, in outer needle zone of 1942, contain 1 sce plus concurrent, exterior, sharp half-lenses.

Here, in contrast with TTP 20-21, multiple diameter flushes for multiple sets of bare-needle zones are present inward on a branch and absent outward near the tip.

TTP 24-13 comprised the inner part and TTP 24-24 the outer part of a single branch cut off January 1, 1943. The inner set of bare-needle zones of 1941 tip growth measured 6.1 cm. and the outer 1.7 cm. For 1942 tip growth, the respective measurements were 6.8 cm. and 2.3 cm. with a terminal bud of 1.7 cm. Terminal bud scale scars separated the two annual flushes, whereas two branches came out from the base of the outer bare zone of 1941, two came out from the outer end of 1941, and two buds were present at the base of the outer bare zone of 1942. In 1942, tip growth had been essentially completed by May 16, only 0.4 cm. having occurred after that date.

Sections *a*, TTP 24-13, 52.9 cm. from base of terminal bud, in 1937 tip growth, contain 1 sce for 1941 and 1 sce plus ddw for 1942. Sections *b*, 41.4 cm. from base of terminal bud, in 1938 tip growth, contain 1 sce for 1941 and 1 sce plus a diffuse lens for 1942. Sections *c*, 29.9 cm. from base of terminal bud, in 1939 tip flush, contain 1 sce for 1941 and 1 sce plus concurrent lenses for 1942. In sections *a* and *b*, postseasonal growth exists rather plentifully whereas in *c* there is none.

As in TTP 24-12, 1941 of TTP 24-13 shows one growth layer for two sets of bare-needle zones, and 1942 shows two growth layers for two sets.

Sections *a* of TTP 24-24, 14.9 cm. from base of terminal bud, in inner needle zone of 1941, contain 1 sce each for 1941 and 1942. Although 1942 tip growth was to that of 1941 as 9.1 is to 7.8, the growth layer for 1942 is much thinner than that for 1941, an inverse relation. Sections *b*, 9.5 cm. from base of terminal bud, in outer needle zone of 1941; sections *c*, 6.3 cm. from base of terminal bud, in inner needle zone of 1942; and sections *d*, 0.3 cm. from base of terminal bud, in outer needle zone of 1942—each shows 1 sce per year. Two sets of bare-needle zones in tip growth are recorded as single flushes in diameter growth. Postseasonal growth which is absent 29.9 cm. from base of terminal bud (sections *c* of TTP 24-13) and apparently still absent at 14.9 cm. from base of terminal bud (sections *a* of TTP 24-24) is present outward on the branch from 9.5 cm. to the base of the terminal bud (sections *b* and *c* of TTP 24-24).

TTP 24-15 comprised the inner and TTP 24-25 the outer part of a single branch cut January 1, 1943. The inner set of bare-needle zones of 1941 measured 6.5 cm., and the outer measured 3 cm. For 1942 tip growth the measurements were respectively 7.7 cm. and 2.8 cm., with a 1.8-cm. terminal bud. Terminal bud scale scars separated the annual flushes; two branches came out at the base of 1941, one at the base of the outer bare zone of 1941 and one between 1941 and 1942; and one bud grew at the base of the outer bare zone of 1942. In 1942, only 0.5 cm. of tip growth occurred after May 16.

Sections *a*, TTP 24-15, 52 cm. from base of terminal bud, in the 1937 tip flush, contain 1 sce for 1941 and 1 sce plus slight ddw for 1942; sections *b*, 37 cm. from base of terminal bud and in the 1938 tip flush, contain 1 sce for 1941 and 1 sce plus extensive ddw plus psq for 1942; and sections *c*, 25 cm. from base of terminal bud and in the 1940 tip flush, contain 1 sce for 1941 and 1 sce plus 2 dce plus psq for 1942.

In TTP 24-25, most sections contain more than 1 sce per year for

1941 and 1942. Sections *a*, from the inner needle zone of 1941, 18 cm. from base of terminal bud, contain 1 sce for 1941 and 1 sce plus patches of psg for 1942; sections *b*, from the outer needle zone of 1941, 11.5 cm. from base of terminal bud, contain 1 sce plus one sharp arc for 1941 and 1 sce plus psg for 1942; sections *c*, from the inner needle zone of 1942, 7.5 cm. from base of terminal bud, contain 1 sce plus psg; and sections *d*, from the outer needle zone of 1942, 0.8 cm. from base of terminal bud, contain 1 sce. Multiple diameter flushes to match multiple tip flushes, as marked by sets of bare-needle zones, exist for 1942 inward from 18 cm. on the branch. Outward from 18 cm. the evidence for multiple diameter growth, although more limited than inward, is present in 1942 and also in 1941.

TTP 24-10 comprised the inner and TTP 24-22 the outer part of a branch cut January 1, 1943. The inner set of bare-needle zones of 1942 tip growth measured 5 cm. and the outer set 1.6 cm. with a terminal bud of 1.5 cm. On May 16, 1942, when artificial freezing was applied, only the inner set of bare-needle zones was present. It is possible that recovery from the impact of frost stimulated a second tip flush. Terminal bud scale scars were absent between the two sets of bare-needle zones. The sections show 1 sce for the two sets of bare-needle zones except for an extra growth layer in the immediate vicinity of 40 cm. inward from base of terminal bud.

The presence of multiple sets of bare-needle zones does not necessarily determine multiplicity in diameter growth. Among the series from which the above illustrations have been taken, there are a few branches bearing only one set of bare-needle zones. TTP 24-14, cut January 1, 1943, did not possess dual sets of bare-needle zones. Sections *a*, 55 cm. from tip of terminal bud, in 1937 tip flush, contain 1 sce plus one sharp lens for 1941 and 1 sce plus ddw for 1942. Sections *b*, 43 cm. from tip, in 1938 tip flush, contain 1 sce for 1941 and 1 sce plus one sharp lens plus ddw plus psg for 1942. Sections *c*, 32 cm. from tip, in 1939 tip flush, contain 1 sce for 1941 and 1 sce plus ddw for 1942. Thus, in TTP 24-14, single sets of bare-needle zones (and one tip flush) accompany multiplicity in diameter growth.

TTP 24-16 and 24-17 possessed single sets of bare-needle zones and single growth layers for each year of 1941 and 1942.

In summary of the bare-needle zone problem it may be said: (1) In the outer part of a branch (say 18 to 20 cm. from base of terminal bud), multiple sets of bare-needle zones seldom are recorded in visible diameter multiplicity. This rather closely parallels the situation where the multiple tip flushes are separated by terminal bud scale scars. (2) Inward on branches, however, there is a much greater

likelihood that tip multiplicity is recorded in the xylem. (3) The presence of a lateral bud, lateral branches, or pistillate cones at the base of an outer bare zone does not signify multiplicity in diameter growth. In later years, therefore, branches do not necessarily arise from intra-annual nodes. With one exception, however, branches with multiple diameter flushes possessed branches, buds, or cones at the bases of the outer bare zones of the particular year.

The relations between tip and diameter flushes in angiosperms resemble those in gymnosperms except that the transitional forms in tip flushes are revealed by leaf scars among angiosperms. Examples come from daily observations and weekly measurements in Maryland at the northwest border of the District of Columbia.

On WCh 1, leaves were out 1.5 cm. by March 25, 1944; by April 26, tip growth averaged 5 to 8 cm. on the tree as a whole; and by May 21, it varied from less than 8 cm. up to 47 cm. Tip growth had attained 60 cm. as a maximum by June 4, but by then about half the branches showed two tip flushes in 1944 growth. The second tip flush, which represented from 40 to 70 percent of the total growth for the season, had developed within the two weeks previous to June 4. Soon after June 4, a storm felled the tree with a clean break below ground level. The stem was constricted at the break to half its diameter at the surface, a handicap no doubt seriously interfering with the passage of food and water and perhaps responsible for the cessation of growth in certain branches.

Tree WCh 2 began growth and followed a course in most ways similar to WCh 1. By June 4, 1944, tip growth on the tree in general varied from 66 to 71 cm. From June 24, which had a few showers, there were high temperatures and no rain until over an inch of rain fell the night of July 13. Another heavy rain fell the night of July 19. By July 23, certain branches had started a second tip flush. Other branches had had continuous growth whereas still others had set small terminal buds. On one branch the leader was growing while its side twigs were in various stages of bursting their terminal buds. Second flushes reached a length of 4 cm. by August 6. They appeared to be active for another month but did not gain perceptibly in length. The leader mentioned for July 23 continued to grow, whereas the side twigs showed no growth beyond initial stages of bud opening. By October 1, tip growth had been completed. By October 22, very few leaves had fallen. Most of them were brown and crisp with reddish veins and had completely fallen from the tree by October 29. In marked contrast to these older leaves, those on the second flushes were

bright green, pliable, and "alive." They remained on the tree throughout most of November but had fallen off completely by the 26th.

The variety of tip behavior on a single tree is illustrated by the observations of September 24 concerning WCh 2. Different branches showed three different types of tip growth:

1. Continuous growth all season.
2. Early flush of growth, then setting of terminal bud; no further extension.
3. Two tip flushes separated by terminal bud scale scars.

There appears to have been no systematic distribution of the stages, all three being noted on one large branch. However, the more primary the branch, the more apt it was to have continuous growth throughout

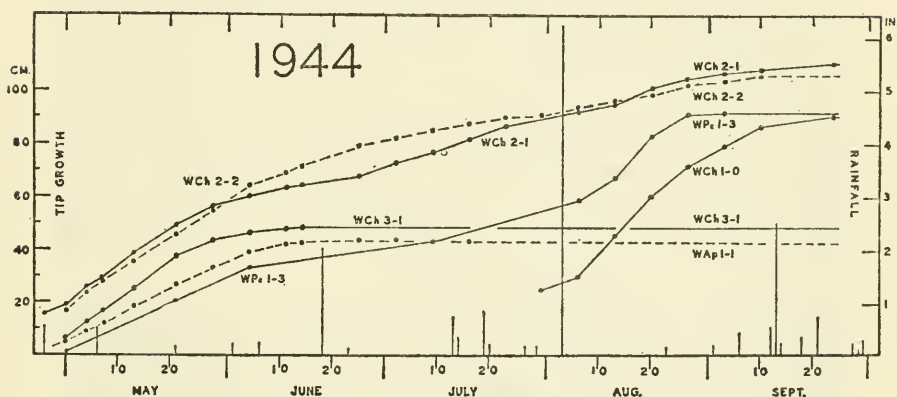


FIG. 43.—Plotted tip growth of Washington trees for 1944.

the season (1, above), and the more secondary or remote the twigs, the more apt they were to grow for a short time before setting a terminal bud (2, above). Most instructive of all, no doubt, were the terminal buds which broke out of their scales when the second flush began and then made no further growth.

Branch WCh 2-2 is an example of continuous tip growth which began in mid-April and ceased between September 3 and 10. Weekly measurements had been made from April 26 to November 26; nearly daily observations were made from the time of initial bud opening until midwinter. Another branch, WCh 2-1, is also an example of continuous growth, and its plotted measurements along with those of WCh 2-2 are given on text figure 43. Even though WCh 2-1 had continuous tip growth during the 1944 season, two plateaus of decreased growth rate are visible, one from about May 28 to June 25 and the second from July 23 to August 13. The graph of WCh 2-2 shows

that the branch responded only a very slight degree to the forces causing a growth slowdown; nonetheless, the tendency is there.

Cross sections made through 1944 tip growth of WCh 2-1 contain 1 sce. In sections *a*, one-third of the way out in the flush, short arcs are present but it can only be assumed that they might correspond to tip growth slowdown.

The second type of tip growth—early setting of terminal bud—was not measured on tree WCh 2. However, an example, WCh 3-1, is well shown on text figure 43. Here tip growth began immediately after April 26, attained 6 cm. by April 30, began to slow down May 28, and ceased by June 14 (June 3 for WCh 3-2). The growth slowdown of branches which were to set early terminal buds occurred at exactly the same time as it did on those branches which were to grow continuously until September. By July 23 the whole tree, WCh 3, was resting, all terminal buds set.

It is of interest to note that sections *a* of WCh 3-1, 12 cm. out from base of 1944 tip flush and 36 cm. from tip of branch, contain 1 sce plus one long diffuse arc whereas the wide-field binocular shows two growth layers on unstained sections. Sections *b*, 9 cm. from tip, contain 1 sce plus one fairly indefinite growth layer which shows as one growth layer under a wide-field binocular.

Tip-growth type consisting of two flushes separated by terminal bud scale scars cannot be shown graphically because weekly measurements did not include such a branch. Those trees and branches not measured were observed constantly, sometimes daily. In general, it is true that times of rapid tip growth coincided on different branches and on different trees and with discrete flushes on branches which set intra-seasonal terminal buds, and that plateaus of growth slowdown (WCh 2-1) coincided with intervals of no growth on branches with multiple tip flushes in one season. Such correspondence holds true, even to the extent that when the third interval of rapid tip growth began on WCh 2-1 a few terminal buds on other branches and other trees expanded sufficiently to separate the bud scales, but grew no farther.

The growth for 1944 in WAp 1-3 comprised two tip flushes of 36.5 cm. and 4 cm. Sections *a*, 3.5 cm. in from the outer end of 1943 tip growth, contain 1 sce for 1943 and 1 dce plus 1 sce for 1944. Sections *b*, 18.2 cm. out from the base of 1944, contain 1 dce and 1 sce, the dce interpreted as belonging to the first tip flush and the sce to the second. Sections *c*, 9 cm. inward from the outer end of first flush, contain 2 dce and 1 sce. The outer dce, two-thirds and more out in the diameter growth of 1944, no doubt corresponds to the first flush of 1944. Sections *d*, 0.5 cm. outward in second 1944, contain a narrow

see which, in thickness, corresponds to the growth layer outward from the dce in the other sections. WAp 1-3 gives a case of two diameter flushes (or growth layers) for two tip flushes in one year.

During 1944, WCh 2-3 formed two tip flushes, the first of 66 cm. and the second of 4 cm. Growth in WCh 2-3 ceased between September 3 and 10. In contrast, many second flushes on other branches of the same tree had ceased growth on or shortly before August 6. This early date corresponds to the second plateau of WCh 2-1, text figure 43, whereas the later date corresponds to the summit plateau. Sections *a* of WCh 2-3, taken 12 cm. out from the base of the first 1944 flush, contain 1 sce. Sections *b*, 7.5 cm. inward from the outer end of first 1944, contain 1 msce plus 1 sce. The msce is almost wholly sharp around the circuit. Why did not the intra-annual msce of sections *b* appear in sections *a*, 46.5 cm. inward on the branch? Did the added diameter growth corresponding to the second tip flush cease inward between *b* and *a*, or did the growth slowdown (or cessation) become less inward until, at *a*, diameter growth was, insofar as visibility is concerned, continuous? Evidence exists for the occurrence of both cases of longitudinal variation in other branches and other trees. Sections *c*, 1 cm. outward from the base of second 1944, contain 1 sce.

Branch WCh 2-6 was observed in regular course during 1944 and especially so in 1945. Tip growth for 1944 contained two flushes, the first "very long" and the second 2.8 cm.; for 1945 tip growth was 26 cm. in one flush. Sections *a*, 17 cm. inward from the outer end of first 1944, contain 2 dce plus 1 sce for 1944 and 1 sce for 1945. One dce is one-third of the way out in 1944 diameter growth whereas the other, which probably corresponds to the second tip flush, is seven-eighths of the way out. Sections *b*, taken just outward from the base of second 1944, contain 1 sce for 1944 and 1 dce (frost induced) plus 1 sce for 1945. In sections *a*, the unstained materials under a wide-field binocular appear to have three growth layers; in sections *b*, probably one growth layer. Both of these wide-field binocular appearances are erroneous. A summary of sections *a* gives 2 sce plus 2 dce for 3 tfs in 2 years; sections *b*, 2 sce plus 1 dce for 2 tfs in $1\frac{1}{2}$ years.

The above examples will perhaps suffice to illustrate the three distinct types of tip growth found among the angiosperms observed, as well as the variations in the relationships of tip growth to diameter growth in any one type. There is, however, a transitional form deserving of mention, the decreased distance between what seemed to be undeveloped leaves. Many of the branches in the top of WCh 2

showed three well-defined zones for 1944 tip growth although they were not separated by terminal bud scale scars. The inner zone, the longest of the three, bore leaves which were set 5 or more cm. apart. The middle zone, up to 19 cm. long, was bare and the "undeveloped leaves" set close together, 1 to 2.5 cm. apart. On the outer zone, 7.5 to 10 cm. in length, the leaves were set 5 or more cm. apart. Thus, based on observations and measurements, the inner and outer zones represented intervals of rapid tip growth whereas the central zones of slow growth were equivalent to the level of terminal bud scale scars on other branches which had two distinct tip flushes, such as WCh 2-4.

Branch WCh 2-5 is a specific example of a transitional growth type between continuous growth and intermittent growth with definite terminal bud scale scars. In the 1944 tip growth, the inner zone of 22 cm., bore leaves and twigs far apart; the middle zone of 19 cm. bore only "undeveloped leaves" which were close together; and the outer zone of 10 cm. bore leaves and twigs far apart except near the tip, where the distances decreased. No terminal bud scale scars appeared within the 1944 tip. Sections *a* from the inner zone of 1944 contain 1 sce plus arcs of diffuse densewood for 1944 and the same for 1945. Sections *b* from the middle zone of 1944 contain 1 sce for 1944 and 1 sce for 1945. Under the wide-field binocular, unstained sections show probably three growth layers. Sections *c* from 1945 tip growth contain 1 sce plus 1 dce, all of which under the wide-field binocular shows as two growth layers. It is quite possible that the arcs of 1944 sections *a* correspond to the growth slowdown represented by the 19-cm. middle zone. On the contrary, 1945 sections *a* also contain arcs, but their definition could not compare with that of the arcs in 1944. WCh 2-5 illustrates the uncertainty of interpretation using unstained sections and low magnification; it also illustrates a transitional growth type.

The peach tree, WPe 1, possessed two types of elongation for second tip flushes in one year, an "offset flush," or the substitution flush of Ratzeburg (1866), and an "in-line flush." In the first case, the original growing tip died and withered because of sun scald or insects, and a new tip emerged from the first axillary bud back of the withered tip. These are second flushes in a certain sense, but do they have an accompanying effect in the xylem? In the second case, later flushes of the same season continued growth outward from the original tips and were separated therefrom by terminal bud scale scars.

WPe 1-1, cut off January 21, 1945, had two offset twigs which arose from the first two axillary buds back of the withered tip of the first flush. Sections were taken from the first flush and from each of the

offset twigs. Each shows 1 sce. On unstained sections, under the wide-field binocular, sections *a* show 1 sce plus a 45° lens.

WPe 1-2, cut off January 21, 1945, had one twig as an offset second flush. Sections *a* from the first flush contain 1 sce plus 1 dce; in contrast, the wide-field binocular shows only one growth layer. Sections *b* and *c* from the offset flush contain 1 sce only.

Although no sections were taken from WPe 1-3, it is of interest because it recorded the effects of a cold spell. An offset flush began May 27, 1945, after the tip of the first flush had died. By June 3, the first offset twig had died and the second had begun to grow, a situation which had become rather general on the tree by June 10. Those branches with continuous growth, as well as those which had set terminal buds by June 10, possessed a zone halfway out on 1945 tip growth where the leaves were closely bunched. One of these even showed terminal bud scale scars. This slowdown of tip growth occurred between April 29 and May 6, a cold interval with heavy frost. Our records say "little or no tip growth" for the 7-day interval.

WPe 1-4, cut off January 21, 1945, contained two sets of terminal bud scale scars in its 1944 tip growth and hence three in-line tip flushes. The first was 12.5 cm. long, the second 14 cm., and the third 11.5 cm. Sections *a*, immediately inward from the end of 1943, contain 1 sce for 1943 and 1 sce plus 1 psce for 1944—all these for four tip flushes for two years. Sections *b*, part way out in first 1944, show 1 sce plus 1 psce for three tip flushes for one year. Sections *c*, from second 1944, contain 1 sce plus 1 psce for two tip flushes for part of one year. Sections *d*, from third 1944, contain 1 sce for 1 tip flush for part of a year. Hence, the first two tip flushes of 1944 correspond to one diameter flush, and the third tip flush corresponds to the second diameter flush.

WPe 1-5 came out as a secondary branch from one whose outer part constituted WPe 1-1. WPe 1-5, cut off June 17, 1945, contained a first flush of 1944, 11 cm. long, a second offset flush of 20 cm., and 1945 as an in-line continuation of second 1944, 6.5 cm. long and dead at the tip. Sections *a*, from first 1944, show 1 sce plus 1 psce for 1944, and 1 inc for 1945, corresponding to three (?) tip flushes for more than one year. Sections *b*, from the second, or offset, flush of 1944, show 1 sce for 1944 and 1 inc for 1945, corresponding to two (?) tip flushes for parts of two years.

WPe 1-6, cut June 17, 1945, contained at least two in-line tip flushes for 1943, two tip flushes (the second offset) for 1944, and one uncompleted flush for 1945. The outer tip flush of 1943 measured 1 cm.; the first flush of 1944 measured 21 cm., the second 24.5 cm.;

and 1945 measured 14.5 cm. Sections *a*, from 3 cm. inward in first 1943, show 1 sce plus 1 psce for two tip flushes for 1943, 1 sce plus 1 psce for two (?) tip flushes for 1944, and 1 inc for 1945, giving five growth layers for five tip flushes for two-plus years. The outer growth layer of 1943 makes up from one-eighth to one-tenth of the annual increment, thus corresponding to the short outer tip flush. In contrast, the outer growth layer of 1944 makes up about one-half the annual increment, a ratio similar to that of the two tip flushes. Sections *b*, from near the base of first 1944, show 1 sce plus 1 psce for two (?) tip flushes for 1944, and 1 inc for 1945, giving three growth layers for three tip flushes for one-plus years. Sections *c*, from base part of the second or offset flush of 1944, show 1 sce for one tip flush for second 1944, and 1 inc for 1945, giving two growth layers for two tip flushes for one-half-plus year. Under the wide-field binocular, sections *a*, *b*, and *c* give 4, 3, and 2 growth layers, respectively. The sharpness of one growth layer differs very little from that of another, whether annual or intra-annual. Vessel size and number vary somewhat, but on the whole this difference is only local.

WPe 1-7, cut off June 17, 1945, contained two (the second offset) tip flushes for 1944 and one incomplete tip flush for 1945, which was a prolongation of the offset flush of 1944. Sections *a*, from 4 cm. inward from the outer end of 1943, show 1 sce for one tip flush for 1943; 1 sce for two tip flushes for 1944; and 1 inc for one tip flush for part of 1945, giving three growth layers for four tip flushes for two-plus years. The wide-field binocular, in comparison, gives three growth layers, the middle one of which has two lenses. Sections *b*, from 5 cm. out in first 1944, show 1 sce for two tip flushes for 1944; and 1 inc for one tip flush for part of 1945, giving two growth layers for three tip flushes for one-plus years. The wide-field binocular gives three growth layers, that of 1944 being double and that of 1945 lacking large vessels. Sections *c* and *d*, from 2 cm. out in second 1944 (one each from two offset branches), show 1 sce for one tip flush for part of 1944; and 1 inc for one tip flush for part of 1945, giving two growth layers for two tip flushes for parts of two years. Here the wide-field binocular gives two growth layers with the addition, in *c*, of a lens of 1944. In sections *b*, the intra-annual of 1944 under the wide-field binocular is revealed under the microscope as a circle of injury, seven-eighths of the way out in the annual increment, and made up of nearly circular local patches of deeply stained tissue surrounded by two to four rows of densewood tracheids either tangential to the section or tangential to the entire patch. Many of the patches contain short cracks. The densewood, the position in the an-

nual increment, and the evidence of injury strongly suggest that this "intra-annual" was the result of the cessation of growth and the death of the growing tip prior to the start of the offset second flush.

The whole matter of growth slowdown and dual tip flushes, both as concerns gymnosperms and angiosperms, may be summarized in outline form as follows:

1. Two tip flushes for one diameter flush.
 - a. Tip flushes separated by terminal bud scale scars.
 - b. Tip flushes represented by sets of bare-needle zones.
2. One tip flush for two diameter flushes.
 - a. One tip flush for two sharp diameter flushes.
 - b. One tip flush for two diameter flushes, one of which is wholly or partly diffuse, the other sharp.
3. Two tip flushes for two diameter flushes.
 - a. Both diameter flushes sharp.
 - b. One diameter flush diffuse, giving a type of transition between 1 and 2.

It is apparent that growth slowdown or actual cessation in gymnosperms is recorded initially in tip growth by a second set of bare-needle zones, and in angiosperms by closely set "undeveloped leaves." Subsequently it is also recorded in diameter growth, if the cessation is sufficiently prolonged or intense.

Secondary xylem in terminal buds.—The existence of secondary xylem in the bud deserves attention because of its characteristics and because of the error it might introduce in the calculation of the annual amount of xylem found for a particular year. Note of this phenomenon as it affects analyses has been made on page 152.

Sections TTP 20-3-c came from the inner part of the terminal bud and, because they were cut December 15, 1939, they can show only the concluding growth of 1939. From pith outward the sections gave the following succession: (1) Primary xylem, four to six cells thick; (2) secondary xylem, 16 to 25 cells thick; (3) cambium; (4) phloem; and (5) outer bark. Under high power the outer four or five cells of the xylem, as seen in cross section, show up as somewhat narrower and more lignified than the inner cells. This is not true of all radial rows. Were the zone of four or five cells within a complete, entire growth layer (as it would have been a year later had the branch not been cut off) it would appear as a faint, highly diffuse intra-annual, if noticed at all. Thus, xylem formed in 1939 would be an integral, but indistinguishable, part of that formed in 1940. The outermost two cells, as well as those only partially differentiated at the time of cutting, were filled with protoplasm at the time the wood samples were placed in preserving fluid. The possible relationships of xylem

to terminal bud in longitudinal sections are shown by the diagram, text figure 44.

Since tip flushes are measured from terminal bud scale scars to terminal bud scale scars located at the bases of the terminal buds, any xylem within the bud, although formed in one year, will augment that of the following year and in any measurements will be taken as part of it.

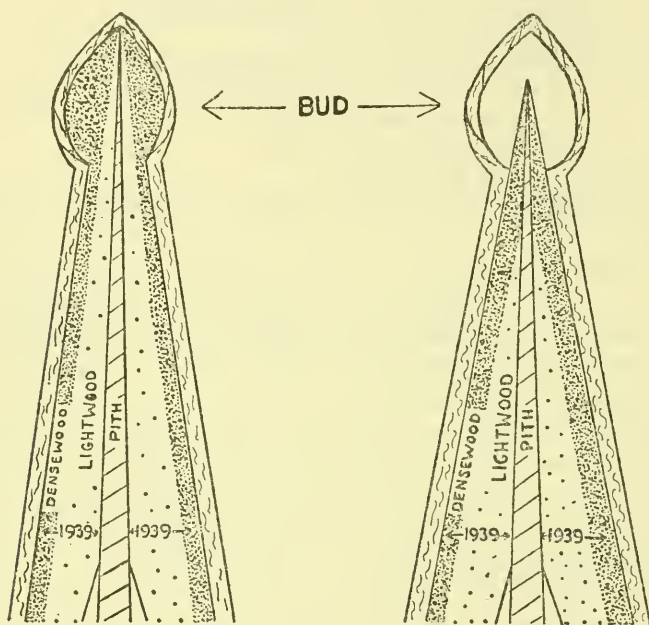


FIG. 44.—TTP 20-3-c. Projection of mature xylem into the terminal bud. At the left, both lightwood and densewood extend into the bud; at the right, only densewood extends into the bud.

Several branches of TTP 22 illustrate xylem within the bounds of a terminal bud formed at least a year prior to the cutting date. TTP 22-1 was cut off on January 17, 1942. Its tip growth had been measured January 4, 1941, and also on the date of cutting. On January 4, 1941, the length of the terminal bud was 3.2 cm. On January 17, 1942, measurements gave 4.3 cm. for 1941 tip growth plus 2.5 cm. for the new terminal bud. Sections *a* came from 1.5 cm. inward from the outer end of 1940 tip flush and contain the following: 1 sce for 1940 and 1 sce plus 1 dce for 1941. The xylem for 1940 constitutes three-fifths of that present in the sections. Sections *b* came from 0.5 cm. outward in 1941 tip growth and therefore within the longitudinal

range of the 3.2-cm. terminal bud. They contain the following: 1 sce pre-1941 and 1 sce plus 1 dce for 1941. The xylem of pre-1941 constitutes one-third of the total xylem present. It does not seem possible that the pre-1941 growth layer could be considered the first growth layer of a multiple 1941 increment nor could it be considered to come within the range of what is normally held to be a *bona fide* tip flush from terminal bud scale scar to terminal bud scale scar. The similarity and identity of position of the dce in sections *a* and *b* positively date it as 1941. Add to this the presence of pre-1941 in sections *a* and the conclusion seems justified that it was xylem in the terminal bud of 1940 formed *during* the season of 1940, even though at cutting date it fell within the range of 1941 tip growth as delimited by terminal bud scale scars and as measured. This is, of course, projecting the lessons of TTP 20-3-c backward a year in time.

Thus we have the experience of finding a previous year's growth layer within the compass of the succeeding year's tip growth. It gives multiplicity somewhat different from that heretofore illustrated.

The situation found in TTP 22-1 is repeated in branches 2, 3, 4, and 6. In two of them the outer margin of the "1940" or pre-1941 growth layer was somewhat indefinite, as in TTP 20-3-c. The following cases of xylem related to terminal buds have been encountered thus far in our work:

1. Densewood reaches to the base of the terminal bud, and lightwood falls short of it.
2. Densewood only extends into the terminal bud.
3. Both lightwood and densewood extend into the terminal bud.

Secondary xylem fails to reach base of terminal bud.—A marked contrast to the phenomenon described above existed in TTJ 4-3 whose tip growth was measured January 30, 1943, February 5, 1944, and July 27, 1944. On the last date, sections were cut. Sections *a* were taken 3 cm. out from the base of 1943 tip growth and contained 1 sce for 1943 and 1 inc for 1944. Although 1943 tip growth measured 13.4 cm., and 1944 measured 8.9 cm., the growth layer, measured at a cross section 3 cm. out from the base of 1943, showed 1943 to possess a width only one-sixth as great as that for 1944. The longer tip growth of 1943 had less diameter growth than the shorter tip growth of 1944. Sections *b*, taken 3 cm. inward from the outer end of 1943 and therefore necessarily sectioning growth of 1943 and 1944, actually contained primary xylem only for 1943 and 1 inc for 1944. In cross section, the primary xylem appeared as detailed patches. Based on the small amount of secondary xylem for 1943 in sections *a* near the base

of 1943 tip growth and its absence in sections *b*, it would seem that a large share of 1943 tip growth consisted of primary xylem and bark only. If a section could be taken some years later at the position of *b* sections, it would be lacking one annual increment. A longitudinal section showing the geometrical design of annual additions of tip growth is commonly oversimplified in view of the two contrasting types of terminal xylem described above.

A stage somewhat intermediate between TTP 20-3-c and TTP 22-1, and TTJ 4-3, is given in TTJ 4-4 which was cut off on July 27, 1944, after having been measured on the same dates as TTJ 4-3. In 1943, TTJ 4-4 put on 12.7 cm. tip growth and in 1944, 8.8 cm. The ratio of these figures is in marked contrast to that of diameter growth. Sections *a*, taken 3 cm. above the base of 1943 tip growth, showed 1 msce for 1943 and 1 sce plus 1 inc for 1944. The growth layer for 1943 averaged one-fourth the thickness of 1944 growth in spite of the fact that 1943 tip growth was nearly 50 percent greater. In sections *b*, taken 3 cm. inward from the outer end of 1943, the 1 msce for 1943 was still half as wide as in *a*. A gradual conical tapering apparently does not characterize the branch; the outer termination of the xylem must be rather abrupt. In sections *b*, farther out, the outer border of the sce of sections *a* has become indefinite.

TTJ 4-5 duplicates TTJ 4-3 by possessing primary xylem only in the outer part of 1943 tip growth.

Measurements of tip growth were made on TTJ 5-3, on March 14, 1942, January 9, 1943, February 5, 1944, and July 28, 1944, and gave 13.8 cm. for 1942, 15.9 cm. for 1943, and 13.6 cm. for 1944 up to July 28, 1944, when the sections were cut. Sections *a*, taken 4 cm. inward from the outer end of 1941 tip growth, show strands of primary xylem for 1941, 1 sce for 1942, 1 msce for 1943, and 1 dce plus 1 inc for 1944. Sections *b*, taken 3 cm. outward from the inner end of 1942, contain a thin growth layer for 1942, 1 msce for 1943, and 1 dce plus inc for 1944. Sections *c*, taken 2 cm. inward from the outer end of 1942, contain strands of primary xylem for 1942, 1 msce for 1943, and 1 dce plus 1 inc for 1944. Sections *d*, taken 3 cm. outward from the base of 1943, contain for 1943 and 1944 the same as did sections *c*. Sections *e* came from 1944 tip growth and contain 1 inc.

Thus, secondary xylem may fall markedly short of the outer end of the tip flush, or it may reach out into the terminal bud.

Lateral buds and dual tip flushes.—This pertains to the relation between lateral buds and dual tip flushes in those cases where the lateral buds arise from, and are a portion of, the terminal bud. Those buds

which are coordinate with, and those which arise at the base of, the terminal bud are not here included.

It had become quite clear by 1942 that the number of tip flushes on the pines was not consistently the same for all branches for any one year; some branches grew one tip flush whereas others grew two. Late in 1942 it was noted that branches with two tip flushes for a certain year had had a lateral bud attached to the terminal bud *above* its base at the close of the previous season. Doak (1935) had recorded such a possible relationship in 1935; Stone and Stone (1943) were to note it in 1943. If it should prove to be true that the presence of a lateral bud *above* the base of the terminal bud predetermines two tip flushes the following season, then such tip flushes are controlled by circumstances in existence during the season prior to the one in which the actual multiple growth occurs.

Our evidence is neither exhaustive nor conclusive. Different cases may be summarized:

1. Lateral buds on terminal—2 tip flushes next season.
2. No lateral buds on terminal—2 tip flushes next season.
3. Lateral buds on terminal—1 tip flush next season.
4. No lateral buds on terminal—1 tip flush next season.

On January 30, 1943, TTP 20-33 had a lateral bud 2.3 cm. above the base of the 2.5-cm. terminal bud. On February 5, 1944, the branch showed tip growth in two flushes, the inner of 6.8 cm. and the outer 2.2 cm. The branch TTP 20-34 bore two lateral buds 1.3 cm. above the base of the 2.4-cm. terminal bud in January 1943. Tip growth for 1943 included two flushes, one of 3.0 and the other of 1.6 cm. TTP 20-40 also illustrates case (1) but with this difference: the first tip flush measured 1.4 cm. and the second 13.3 cm. At the start of the season, the 2.8-cm. terminal bud bore a lateral bud 2.3 cm. above its base. If this lateral bud did have genetic significance for future tip flushes, then its position longitudinally on the terminal bud had no significance as regards the relative lengths of the two subsequent tip flushes. TTP 23-9 carried two lateral buds 1.3 cm. above the base of the 2.3-cm. terminal bud prior to the 1943 season. At the end of that season, tip growth showed an inner flush of 4.2 cm. and an outer flush of 1.2 cm. The two lateral buds which were *on* the terminal bud had expanded into two branches, thus apparently establishing a direct genetic connection between the lateral buds and the subsequent dual tip flushes. Yet this is just one example.

Examples under case (2) are as numerous as those under case (1) among the branches devoted to special study. In TTP 20-16, tip growth for 1942 comprised an inner flush of 7.3 cm. and an outer one

of 2 cm. (growth for 1943 classified under case (4)). Growth for 1943 in TTP 20-27 included an inner flush of 2 cm. and an outer flush of 2.3 cm. TTP 20-31 presented an interesting circumstance in its growth for 1943. On January 30, 1943, a large lateral bud arose from the base of the terminal bud. During 1943 the two buds developed into two coordinate branches. One of these contained two tip flushes, the inner 5.6 and the outer 2 cm.; the other branch contained one tip flush of 6.8 cm. Thus cases (2) and (4) are as intimately connected, it seems, as any two branches could relate them. TTP 20-36 on January 30, 1943, carried two lateral buds at the base of the terminal bud and two lateral buds 2 cm. *below* the base. During 1943, the four lateral buds grew into four branches of one tip flush each, whereas the original branch grew two tip flushes, an inner of 11.6 cm. and an outer of 1.6 cm.

The series of branches under special study gave one example of case (3). Branch TTP 20-38, on January 30, 1943, had two lateral buds 1.7 cm. above the base of the 2.3-cm. terminal bud. During 1943 the branch lengthened by one tip flush only. One lateral bud left no trace; the other grew into a 5.1-cm. lateral branch.

Examples of case (4) are by far the most numerous. They include all branches of the series in which the examples of the other cases were scattered.

From the rather slight evidence at hand we may conclude, first, that the presence of lateral buds on the terminal bud may or may not be followed by the formation of two tip flushes; and, second, that the absence of such lateral buds does not preclude the formation of two tip flushes.

A consideration of buds in their relations to tip flushes necessitates the mention of TTP 23-11. The original terminal bud of 1942, in January 1943, was dry and bent to the side. Taking its place, a lateral bud at the base of the former had very nearly assumed a position proper to a terminal bud. Very little evidence remained to show that the new terminal had once been a lateral bud, and, in February 1944, the only evidence was a slight bend in the branch at the start of 1943 growth. Because this evidence of the conversion of a lateral bud into a leader was virtually obliterated in one year, it raises the questions of how often this may happen and also how often the tip growth of one or two years may be lost when estimating the age of a branch by the number of terminal bud scale scars. It would be rather difficult to explain the discrepancy between age as determined by terminal bud scale scars and age as determined by number of growth layers.

RELATIONS AMONG BRANCHES OF THE SAME TREE

A lack of consistency in the unity or multiplicity in growth layers of corresponding years in different branches has been mentioned when pertinent heretofore. Such lack is to be expected and may be characteristic of trees grown in the extreme lower forest-border region. Several questions arise from a study of branch materials: (1) Do the branches within a single tree correspond with each other; and if so, to what extent? (2) Does the amount of correspondence vary from tree to tree under the same general environment? (3) Is there a similarity among branches according to the year? (4) What is the influence of the environment?

Before details are given, several points should be reemphasized: (1) "Serial" sections were taken at unequal intervals along the branches; (2) sections were taken on different dates, from 1939 to 1945; (3) sections contained different series of growth layers; and (4) the trees grew at the extreme lower forest border.

The first question mentioned above was, "Do the branches within a single tree correspond with each other; and if so, to what extent?" Much detail could be given because, in fact, each section of every branch was examined, dated, and all growth layers identified and described. All these results exist in charted form. From them the following typical examples are abstracted.

In addition, the tables here given show the nature and amount of multiplicity and the variation longitudinally on the different branches. Some details of certain branches may not seem to agree with those given heretofore; this disagreement is due to the uniting of certain growth-layer types or to selecting certain types for emphasis.

Consider the year 1940, for Con T 1 (table 142): four branches have multiplicity; the year 1941: three branches have unity and five have multiplicity; the year 1942: six branches have unity and two have multiplicity. If we multiply the number of branches by the number of years in those branches, we obtain the number of branch-years. This gives 20 branch-years, of which 9 have unity and 11 have multiplicity. Thus, 90 percent of the branch-years (i.e., 9 unity plus 9 multiplicity, making 18 out of the total 20 branch-years) offset each other in respect to unity and multiplicity—they cancel. The remaining 2 out of 20 branch-years, or 10 percent, represents the amount of agreement.

The year 1938 for TTAp 2 (table 143) has all four branches multiple; 1939, all four branches multiple. Agreement is 100 percent, that is, all branches have multiple growth layers for all years.

The year 1937 for TTC 34 (table 144), one branch has unity whereas the other two have multiplicity; 1938, one branch has unity whereas three have multiplicity; 1939, four with multiplicity; and 1940, four with multiplicity. Of branch-years there are 15, of which 2 have unity and 13 have multiplicity. For these four branches with the years represented, there is an agreement of 73 percent.

TABLE 142.—*Con T 1*

	I-5	I-6	I-7	I-8
1940		a. 1 sce + d arcs b. 1 sce		
1941	a. 1 sce b. 1 sce	a. 2 sce b. 2 sce c. 2 sce d. 1 sce	a. 2 sce + d arcs b. 2d 1941: 1 sce	a. 2 psce b. 2d 1941: 1 dce
1942	a. 1 sce + 1 dce b. 1 sce + 1 dce c. 1 sce + 1 dce d. 1 dce	a. 1 sce b. 1 sce c. 1 sce d. 1 sce e. 1 sce f. 1 sce	a. 1 sce + d arcs + psge b. 1 sce + d arc c. 1 psce + 3-5 + d arcs d. 1 psce + 3-5 + d arcs	a. 1 msce b. 1 dce c. 1 dce
	I-10	I-11	I-12	I-13
1940		a. 2 sce b. 1 sce	a. 1 or 2 psce + dce +idw b. 1 psce	3d 1940: a. 1 psce b. 1 psce
1941	2d 1941: a. 2 sce + 1 msce + dce's b. 2 sce + dce's	a. 1 sce b. 1 sce c. 1 sce	a. 2 or 1 psce + dce's b. 1 psce c. 1 psce	a. 1 psce b. 1 psce c. 1 psce
1942	a. 1 sce b. 1 sce c. 1 sce d. 1 sce	a. 1 sce b. 1 sce c. 1 sce d. 1 sce e. 1 sce	a. 1 psce b. 1 psce c. 1 psce d. 1 psce e. 1 psce	a. 1 psce b. 1 psce c. 1 psce d. 1 psce e. 1 psce

The year 1936 for TTP 20 (table 145) has three multiple; 1937, all five multiple; 1938, two with unity, three with multiplicity; and 1939, two with unity, two with multiplicity (branch 20-4 for 1939 ignored because growth had not been completed). There are 17 branch-years of which 4 have unity and 13 have multiplicity. Agreement among the branches is 53 percent.

TABLE 143.—*TTap* 2

	2-1	2-2	2-3	2-4
1938	a. 2 sce	a. 1 sce + 1 dce b. 1 sce	a. 1 sce + 1 msce b. 1 sce + 1 d $\frac{1}{2}$ L	a. 1 sce + 1 msce b. 1 sce
1939	a. 2 sce b. 2 sce c. 2 sce	a. 2 sce + d arcs + $\frac{1}{2}$ L's b. 2 sce + d arcs + $\frac{1}{2}$ L's c. 2 sce d. 2 sce	a. 1 sce + 1 sL + 1 msce + 3 dL + 1 d $\frac{1}{2}$ L b. 1 sce + 1 sL + 3 dL + 1 d $\frac{1}{2}$ L c. 2 sce + 1 dce d. 2 sce + 1 dce	a. 1 sce + 1 sL b. 1 sce + 1 sL + 1 dL c. 2 sce + ddw d. 2 sce + ddw

TABLE 144.—*TTC* 34

	34-1	34-2	34-3	34-4
1937		a. 1 sce + 1 dL b. 1 sce c. 1 sce	a. 1 sce b. 1 sce c. 1 sce d. 1 sce	a. 1 sL + 1 msce b. 1 sL + 1 msce c. 1 sce
1938	a. 1 sce b. 1 sce c. 1 sce	a. 2 sce + 1 sL + 1 msce + 1 dL b. 2 sce + 2 sL + 1 msce + 1 dL c. 1 sce + 2 sL + 2 msce	a. 1 sce + 1 sL b. 1 sce c. 1 sce + 1 msce + 1 dL d. 1 sce	a. 1 sce + 1 sL + 1 msce b. 1 sce + 1 sL + 1 msce c. 1 sce d. 1 sce
1939	a. 1 sce + 1 sL b. 1 sce + 1 sL c. 1 sce + 1 msce d. 1 sce + 1 msce	a. 1 sce b. 1 sce + 1 sL c. 1 sce + 1 dL	a. 1 sce + 1 sL b. 1 sce + 1 sL c. 1 sce + 1 sL d. 1 sce + 1 msce	a. 1 sce + 1 sL b. 1 sce + 1 sL c. 1 sce d. 1 sce + 1 sL
1940	a. 1 sce + 1 sL b. 1 sce + 1 sL c. 1 sce + 1 sL d. 1 sce + 1 sL	a. 1 sce + 1 sL + 1 d arc b. 1 sce + 1 sL + 2 msce c. 1 sce + 2 dL + arc	a. 1 sce + 1 sL b. 1 sce + 1 sL c. 1 sce + 1 sL d. 1 sce + 1 sL	a. 1 sce + 1 sL + 1 dL b. 1 sce + 1 sL + 1 dL c. 1 sce + 1 sL d. 1 sce + 1 sL

TABLE 145.—*TTP* 20

	20-1	20-2	20-3	20-4	20-6
1936	a. 1 sce + 1 dce + 1 psL	Last 1936: a. 1 dce		a. 1 psce + 1 msce + 1 dL	
1937	a. 1 sce + 1 sL + 1 msce	a. 2 sce + 2 dL b. 2d 1937: 1 sce	a. 2 sce + 1 psL + 1 dL b. 2d 1937: 1 dce	a. 2 msce + 2 msL b. 1 sce + 2 dce + ddw	a. 1 sce + 1 dce + ddw
1938	a. 1 sce + 1 d arc b. 1 dce	a. 1 sce + 1 dce b. 2 dce c. dw	a. 1 sce b. 1 psce	a. 2 sL + 1 msce b. 1 msce	a. 1 sce b. 1 sce
1939	a. 1 sce b. 1 sce + 1 dL + psq	a. 1 sce + 1 dL b. 1 sce + 1 msce c. 1 sce + 1 dce (?) d. inc	a. 1 psL b. 1 psL c. 1 pspee	a. inc L b. inc	a. 1 sce b. 1 sce

TABLE 146.—TTP 24

	24-1	24-2	24-3	24-4	24-12
1936		a. 1 sce b. 1 sce	a. 2 sce + 1 dce b. 3 sce + 2 dce c. 2 sce + 1 dce		
1937		a. 1 sce + 1 dce b. 1 sce c. 1 sce	a. 2 sce b. 2 sce c. 2 sce d. 2 sce	a. 1 sce b. 1 sce c. 1 sce	a. 1 sce + 2 dce
1938	a. 1 sce b. 1 sce	a. 1 sce b. 1 sce c. 1 sce d. 1 sce	a. 1 dce b. 1 dce c. 1 sce d. 1 sce	a. 1 sce b. 1 sce c. 1 sce d. 1 sce	a. 1 sce b. 1 sce
1939	a. 1 msce b. 1 sce c. 1 sce	a. 1 sce b. 1 sce c. 1 sce d. 1 sce	a. 1 msce b. 1 msce c. 1 sce d. ddw	a. 1 sce b. 1 sce c. 1 sce d. 1 sce	a. 1 sce b. 1 sce c. 1 sce + 1 psce
1940	a. 1 sL + 1 msce + 1 psce b. 1 sce + 1 dce + 1 sL + 1 dL c. 1 sce	a. 1 sce + 1 msce b. 1 sce + 1 psce c. 1 sce + 2 dce d. 1 sce + 2 dce	a. 1 msce b. 1 msce c. 1 msce d. 1 msce	a. 1 msce + 1 psce + 1 dce b. 1 msce + 1 psce + 1 dce c. 1 msce + 1 psce + 1 dce d. 1 sce + 2 dce	a. 1 sce + 1 psce b. 1 sce + 1 dce c. 1 sce + 1 dce

The year 1936 for TTP 24 (table 146) has one with unity and one with multiplicity; 1937, one with unity and three with multiplicity; 1938, all five with unity; 1939, four with unity and one with multiplicity; and 1940, one with unity and four with multiplicity. Branch-years number 21, of which 12 have unity and 9 have multiplicity. Among these branches, agreement is 14 percent.

The year 1944 for WAp 1 (table 147) has one with unity and one with multiplicity. This gives 100 percent disagreement.

The year 1944 of WPe 1 (table 148) has two branches with unity, four with multiplicity. Agreement is 33 percent.

The year 1932 of XSC 1 (table 149) has two branches with multiplicity; 1933, three branches multiple; 1934, three multiple; 1935, three multiple; 1936, four multiple; 1937, four multiple; 1938, four multiple; and 1939, four multiple. There is 100 percent agreement.

The year 1936 of XSC 2 (table 150) has all three branches multiple; 1937, all three multiple; 1938, one with unity and two with multiplicity; and 1939, all three multiple. There are 12 branch-years, of which 1 has unity and 11 multiplicity, giving an agreement of 83 percent.

The year 1937 for XSC 8 (table 151) has all six branches with unity; 1938, all six multiple; 1939, one with unity, five with multiplicity; and 1940, all six multiple. Of the 24 branch-years, 7 have unity and 17 have multiplicity. This gives an agreement of 42 percent.

The year 1937 of XSC 12 (table 152) has two branches with unity and one with multiplicity; 1938, all three multiple; 1939, one with unity and two with multiplicity; and 1940, all three multiple. Of the 12 branch-years, 3 show unity and 9 multiplicity. This comes out as an agreement of 50 percent. XSC 12 (table 152) illustrates well what has been pointed out heretofore concerning longitudinal variation: an increase inward in numbers or area of sharply bordered growth layers within a single year (12-1, 1938; 12-2, 1938), an increase outward (12-1, 1939; 12-3, 1937), no change within the compass of the sections (12-2, 1939, 1940), or a change in both directions (12-1, 1940).

The year 1937 of XSC 13 (table 153) has two branches with unity and one with multiplicity; 1938, all three multiple; 1939, all three multiple; 1940, one with unity and two with multiplicity; and 1941 has two branches with multiplicity. Of the 14 branch-years, 3 have unity and 11 have multiplicity. This gives an agreement of 57 percent. The year 1941 of XSC 13 (table 153) differs from previous years in that all three branches were frozen artificially June 14, 1941, at about the same temperature and for approximately the same length of time. Branch XSC 13-1 was permitted six days of recovery before being cut

TABLE 147.—*WAp* I

	I-1	I-3
1943	a. I sce + I sL	a. I sce
1944	a. I sce	a. I sce + I dce
	b. I sce	b. I sce + I dce
	c. I sce	c. I sce + 2 dce
		d. 2d 1944: I sce

TABLE 148.—*WPe* I

	I-1	I-2	I-4	I-5	I-6	I-7
1944	a. I sce	a. I sce + I dce	a. I sce + I psce	a. I sce + I psce	a. I sce + I psce	a. I sce
	b. I sce	b. I sce + I dce	b. I sce + I psce	b. I sce	b. I sce + I psce	b. I sce
	c. I sce	c. I sce	c. I sce + I psce		c. I sce	c. I sce
			d. 3d 1944: I sce			d. I sce

TABLE 149.—XSC I

	I-1	I-2	I-3	I-4
1932	a. 2 sce + 1 psce b. 1 sce	a. 2 sce + 1 sL + 1 msL b. 2 sce + 1 psce		
1933	a. 1 sce + 1 sL b. 2 sce + 1 psL	a. 2 sce + 1 s $\frac{1}{2}$ L b. 2 sce + 1 psL + 1 s $\frac{1}{2}$ L + 3 ddw		a. 1 sce + ddw
1934	a. 1 sce b. 2 sce + 1 psL	a. 1 sce + dL's b. 2 sce + 1 d arc		a. 1 sce + 1 sL + 1 dL
1935	a. 4 sce + 1 psL + 1 s $\frac{1}{2}$ L b. 2 sce + 1 dce	a. 2 sce + 2 sL b. 3 sce + 1 psL		a. 2 sce + 3 sL + 1 dL
1936	a. 1 msce + 1 psce b. 3 dce	a. 1 sce + 1 sL + 2 msce b. 4 sce + 5 sL	a. 1 sce + 2 sL b. 1 sce + 2 sL c. 1 sce + 2 sL	a. 2 sce
1937	a. 2 sce + 2 $\frac{1}{2}$ L b. 1 psce + 2 dce	a. 2 sce + 2 sL + 2 psL + 2 d $\frac{1}{2}$ L + 1 s $\frac{1}{2}$ L + ddw b. 2 sce + 2 sL + 2 msL + 3 d $\frac{1}{2}$ L + 1 s ddw	a. 1 sce + 2 sL b. 1 sce + 2 sL c. 1 sce + 2 sL	a. 2 sce + 4 sL + 1 dL
1938	a. 1 sce + 1 psL b. 1 sce + 2 sL + 1 dL	a. 1 sce + 1 psce b. 1 sce + 1 dL	a. 5 sce + 1 sL b. 5 sce + 1 sL c. 5 sce + 1 sL	a. 1 sce + ddw
1939	a. 1 sce + 1 sL + 3 psL + 1 dL b. 1 sce + 1 sL + 1 msL + 1 s $\frac{1}{2}$ L + 1 d $\frac{1}{2}$ L	a. 2 sce + 1 sL + 1 msL + 1 d arc + 1 s $\frac{1}{2}$ L b. 1 sce + 3 sL + 1 dL + 1 s $\frac{1}{2}$ L + 2 d $\frac{1}{2}$ L	a. 1 sce + 2 sL b. 1 sce + 2 sL c. 1 sce + 2 sL	a. 2 sL + 1 msce + 1 msL

from the tree; branch XSC 13-2 was cut 13 days after freezing; and 13-3, 27 days after. Thus, the amount of growth as well as the completeness of the growth layers depended upon the length of the period of recovery.

The year 1937 for XSP 1 (table 154) has two branches with unity; 1938, two multiple; 1939, two with unity; and 1940, two multiple. There are eight branch-years of which four are single and four multiple. Agreement is zero.

TABLE 150.—XSC 2

	2-1	2-2	2-3
1936	a. 1 sce + 7 sL b. 1 sce + 7 sL	a. 5 sce + 3 sL + 1 msL b. 5 sce + 3 sL + 1 msL c. 5 sce + 4 sL	a. 2 sL + 6 msce b. 2 sL + 6 msce c. 2 sL + 6 msce
1937	a. 3 sce + 2 sL b. 3 sce + 2 sL	a. 2 sce + 1 dce b. 2 sce + 1 dce c. 2 sce + 1 dce	
1938	a. 1 sce b. 1 sce	a. 1 sce + 2 sL + arcs b. 1 sce + 1 sL + 1 dL c. 1 sce + 1 sL	a. 1 sce + 1 sL + ddw b. 1 sce + 1 sL + ddw c. 1 sce + 1 sL + ddw
1939	a. 1 sce + 2 sL b. 1 sce + 2 sL + 1 msL	a. 1 sce + 1 sL b. 1 sce + 1 sL c. 1 sce + 1 sL + 1 msL	a. 1 sce + 1 sL + ddw b. 1 sce + 1 sL + ddw c. 1 sce + 1 sL + ddw

The year 1936 for XSP 2 (table 155) has one branch with unity and two with multiplicity; 1937, two with unity and one with multiplicity; 1938, all three multiple; and 1939, one with unity and two with multiplicity. There are 12 branch-years of which 4 have unity and 8 have multiplicity, giving an agreement of 33 percent.

In the above detailed examples, agreement among the branches of each tree varies from zero to 100 percent. A tabular summary of the trees and branches used in the foregoing examples is given in table 156.

Rather than extend table 156 to include all trees and all branches, table 157 has been prepared to include the entire mass of data as a percentage summary.

TABLE 151.—XSC 8

	8-1	8-2	8-3	8-4	8-5	8-6
1937	a. 1 sce b. 1 sce	a. 1 sce b. 1 sce c. 1 sce	a. 1 sce b. 1 sce c. 1 sce	a. 1 sce b. 1 sce c. 1 sce	a. 1 sce b. 1 sce c. 1 sce	a. 1 sce b. 1 sce c. 1 sce
1938	a. 2 sce + 1 psce + 2 msce b. 1 sce + 3 msce	a. 1 sce + 2 s arcs b. 1 sce + 2 d arcs c. 1 sce + 2 d arcs	a. 1 sce + 2 d arcs + ddw b. 1 sce + 1 dce + ddw c. 1 sce	a. 1 sce + 1 sL + 1 msce + 1 psce b. 1 sce + 1 sL + 1 msce + 1 psce c. 1 sce + 1 sL + 1 msce + 1 psce	a. 1 sce + 1 sL + 1 msce + 1 psce b. 1 sce + 1 sL + 1 msce + 1 psce c. 1 sce + 1 sL + 1 msce + 1 psce	a. 1 sce + 1 sL + 1 msce + 1 psce b. 1 sce + 1 sL + 1 msce + 1 psce c. 1 sce + 1 sL + 1 msce + 1 psce
1939	a. 1 sce b. 1 sce	a. 1 sce b. 1 sce c. 1 sce + ddw	a. 1 sce + 1 msce + 1 dL + 1 s arc b. 1 msce + 1 psce + 1 psL c. 1 sce + 1 psce + 1 dce	a. 1 sce + 2 sL + 1 dL b. 1 sce + 2 sL + 1 dL c. 2 sce + 2 sL + 1 dL	a. 1 sce + 2 sL + 1 dL b. 1 sce + 2 sL + 1 dL c. 2 sce + 2 sL + 1 dL	a. 1 sce + 2 sL + 1 dL b. 1 sce + 2 sL + 1 dL c. 2 sce + 2 sL + 1 dL
1940	a. 1 sce + 4 sL b. 2 sce + 3 sL	a. 1 dL b. 1 dL c. 1 dL + ddw	a. 1 sce + 1 sL + 1 s arc + 1 d arc b. 1 sce + 1 sL + 1 psce + 1 dL c. 1 sce + 1 sL + 1 psce	a. 2 sce + 1 msce + 1 s arc b. 2 sce + 1 msce + 1 s arc c. 2 sce + 1 msce + 1 s arc	a. 1 sce + 1 msce + 1 s arc b. 1 sce + 1 msce + 1 s arc c. 1 sce + 1 msce + 1 s arc	a. 1 sce + 1 msce + 1 s arc b. 1 sce + 1 msce + 1 s arc c. 1 sce + 1 msce + 1 s arc

The second column (a) of table 157 carries the total number of branches taken from a tree. The third column (b) carries the sum of all years in all branches. The fourth and fifth columns (c and d) give the percentage of branch-years with single diameter flushes and those

TABLE 152.—XSC 12

	12-1	12-2	12-3
1937	a. 1 sce	a. 1 sce	a. 1 sce + 1 sL + 1 d arc
	b. 1 sce	b. 1 sce	b. 1 sce + 1 sL + 1 d arc
	c. 1 sce	c. 1 sce	c. 2 sce + 1 d arc + ddw
		d. 1 sce	
1938	a. 3 sce + 1 dL + dw	a. 1 sce + 1 msce + 1 psce + 2 sL	a. 1 sce + 1 dce + 1 sL
	b. 3 sce + 1 dL	b. 1 sce + 1 msce + 1 psce + 2 sL	b. 1 sce + 1 dce + 1 sL
	c. 1 sce	c. 1 sce + 1 msce + 1 psce + 2 sL	c. 1 sce + 1 dce + 1 msce
		d. 1 sce + 2 dce + 1 msL + ddw	
1939	a. 2 sce + 1 dL + ddw	a. 2 sce + 1 dL + ddw + arcs	a. 1 psce
	b. 2 sce + 1 dL + ddw	b. 2 sce + 1 dL + ddw + arcs	b. 1 psce
	c. 2 sce + 1 sL + 1 dL	c. 2 sce + 1 dL + ddw + arcs	c. 1 psce
	d. 2 sce + 1 sL + 1 dL	d. 2 sce + 1 dL + arcs	
1940	a. 1 sce + 1 sL + 1 msce + 1 d $\frac{1}{2}$ L	a. 2 sce + 1 sL + ddw	a. 1 psce
	b. 1 sce + 1 sL + 1 msce + 1 d $\frac{1}{2}$ L	b. 2 sce + 1 sL + ddw	b. 1 psce + 1 dL
	c. 1 sce + 1 msL + 1 d $\frac{1}{2}$ L + 1 psce	c. 2 sce + 1 sL + ddw	c. 1 psce
	d. 1 sce + 1 dce + 1 psL + 1 d $\frac{1}{2}$ L	d. 2 sce + 1 sL + ddw	

with multiple flushes. The sixth column (e) gives the percentage of branches agreeing with each other in each tree and is obtained by taking the difference between the values of (c) and (d). Here, too, the range of agreement attains a maximum, zero to 100 percent. In those cases where agreement among the branches of a tree is extreme, either zero or 100 percent, the number of branches from any one tree

is 5 or less, and in 6 out of the 14 cases only 2 branches were taken. The reverse is not true; that is to say, a tree from which only a few branches were taken did not necessarily have an extreme of agreement

TABLE 153.—XSC 13

	13-1	13-2	13-3
1937	a. 1 sce b. 1 sce	a. 1 sce b(1). 1 sce b(2). 1 sce c. 1 sce d. 1 sce	a. 1 sce + 1 dce b. 1 sce + 1 dce c. 1 sce d. 1 sce
1938	a. 3 msce + 1 psce + ddw b. 2 sce c. 1 sce	a. 1 sce + 1 msce + 1 s arc b(1). 1 sce + 1 msce + 1 dL + 1 s arc b(2). 1 sce + 1 psce + 1 dL + 1 s arc c. 1 sce + 1 dce + 1 dL + 1 s arc d. 1 sce + 1 dce + 1 dL + 1 s arc	a. 1 sce + 1 sL + 1 msL b. 2 sce + 1 msce c. 1 sce + 1 sL + 1 msL d. 1 sce + 1 sL + 1 msL
1939	a. 3 sce + 1 dce b. 3 sce + 1 msL + 1 dce + ddw c. 3 sce + 1 msL	a. 2 sce + 1 sL + 1 dL b(1). 2 sce + 1 sL + 2 dL b(2). 2 sce + 2 sL + 1 dL c. 2 sce + 2 sL + 1 dL d. 2 sce + 2 sL + 1 dL	a. 1 sce + 1 sL b. 1 sce + 1 sL c. 1 sce + 2 sL d. 1 sce + 1 sL
1940	a. 1 sce + ddw b. 1 sce + 1 msL + 1 dL + ddw c. 1 sce + 1 msL + 1 dL	a. 1 sce + 1 s $\frac{1}{2}$ L + 1 d $\frac{1}{2}$ L b(1). 1 sce + 1 s $\frac{1}{2}$ L + 1 d $\frac{1}{2}$ L b(2). 1 sce + 1 s $\frac{1}{2}$ L + 1 d $\frac{1}{2}$ L c. 1 sce + 1 s $\frac{1}{2}$ L + 1 d $\frac{1}{2}$ L d. 1 sce + 1 s $\frac{1}{2}$ L + 1 d $\frac{1}{2}$ L	a. 1 sL b. 1 sL c. 1 sL d. 1 sL
1941	a. inc b. inc c. inc	a. 1 pce + psq b(1). 1 ce + psq b(2). 1 pce + psq c. 1 pce + psq d. 1 pce + psq	a. 1 sce + psq b. 1 sL + psq c. 1 spce + psq d. 1 sce + psq

or disagreement. Hence, the trees with few branches are felt to be of significance because the branches were taken at random insofar as unity and multiplicity were concerned.

TABLE 154.—XSP 1

	1-1	1-2
1937	a. 1 sce b. 1 sce c. 1 sce	a. 1 sce
1938	a. 1 sce + 1 sL b. 1 sce + ddw c. 1 sce	a. 1 sce + ddw
1939	a. 1 sce b. 1 sce c. 1 sce	a. 1 sce b. 1 sce
1940	a. 1 sL + inc L b. 1 sce + 1 sL + inc c. inc	a. 2 sce + 1 sL + ce b. 2 sce + 1 sL + ce

TABLE 155.—XSP 2

	2-1	2-2	2-3
1936	a. 2 sce + 1 dL b. 1 sce	a. 1 sce	a. 1 sce + ddw
1937	a. 1 sce + arcs b. 1 sce c. 1 sce	a. 1 sce	a. 1 sce
1938	a. 2 sce + ddw b. 2 sce + 2 dL c. 2 sce	a. 1 sce + 1 sL	a. 2 sce
1939	a. 1 sce + 1 dL b. 1 sce + 1 sL c. 2 sce	a. 1 sce	a. 2 sce

TABLE 156.—Summary of tables 142 to 155, showing the number of branches with one diameter flush and the number with more than one, for given years

Tree	Number of branches	Number with one diam. flush	Number with more than one diam. flush	Date
Con T 1.....	4	0	4	1940
	8	3	5	1941
	8	6	2	1942
TTAp 2.....	4	0	4	1938
	4	0	4	1939
TTC 34.....	3	1	2	1937
	4	1	3	1938
	4	0	4	1939
	4	0	4	1940

Continued

TABLE 156.—*Concluded*

Tree	Number of branches	Number with one diam. flush	Number with more than one diam. flush	Date
TTP 20.....	3	0	3	1936
	5	0	5	1937
	5	2	3	1938
	4	2	2	1939
TTP 24.....	2	1	1	1936
	4	1	3	1937
	5	5	0	1938
	5	4	1	1939
	5	1	4	1940
WAp 1.....	2	1	1	1944
WPe 1.....	6	2	4	1944
XSC 1.....	2	0	2	1932
	3	0	3	1933
	3	0	3	1934
	3	0	3	1935
	4	0	4	1936
	4	0	4	1937
	4	0	4	1938
	4	0	4	1939
XSC 2.....	3	0	3	1936
	3	0	3	1937
	3	1	2	1938
	3	0	3	1939
XSC 8.....	6	6	0	1937
	6	0	6	1938
	6	1	5	1939
	6	0	6	1940
XSC 12.....	3	2	1	1937
	3	0	3	1938
	3	1	2	1939
	3	0	3	1940
XSC 13.....	3	2	1	1937
	3	0	3	1938
	3	0	3	1939
	3	1	2	1940
	2	0	2	1941
XSP 1.....	2	2	0	1937
	2	0	2	1938
	2	2	0	1939
	2	0	2	1940
XSP 2.....	3	1	2	1936
	3	2	1	1937
	3	0	3	1938
	3	1	2	1939

TABLE 157.—*Summary of all branches, to show the percentage of branches in agreement in each tree*

Tree	Number of branches (a)	Number of branch-years (b)	Type of flush %		Flush agreement % (e)
			Single (c)	Multiple (d)	
Con P 2.....	2	2	50	50	0
Con T 1.....	19	37	59	41	18
Con T 2.....	15	37	41	59	18
MP 1.....	2	3	0	100	100
SA 1-5.....	5	26	50	50	0
TTAp 1.....	4	8	0	100	100
TTAp 2.....	4	8	0	100	100
TTC 1.....	2	4	0	100	100
TTC 5.....	11	54	28	72	44
TTC 12.....	3	18	17	83	66
TTC 30.....	2	5	20	80	60
TTC 33.....	17	41	15	85	70
TTC 34.....	26	58	28	72	44
TTC 35.....	7	11	27	73	46
TTC 36.....	8	33	12	88	76
TTC 37.....	5	5	100	0	100
TTCw 1.....	6	10(?)	60	40	20
TTJ 2.....	14	48	31	69	38
TTJ 4.....	4	5	80	20	60
TTL 3.....	4	5	80	20	60
TTL 5.....	4	6	0	100	100
TTM 1.....	9	19	32	68	36
TTM 3.....	3	4	50	50	0
TTP 20.....	39	78	24	76	52
TTP 21.....	10	42	48	52	4
TTP 22.....	5	10	60	40	20
TTP 23.....	20	37	43	57	14
TTP 24.....	27	97	58	42	16
WAp 1.....	2	3	33	67	34
WCh 2.....	4	6	0	100	100
WCh 3.....	2	2	0	100	100
WPc 1.....	6	7	29	71	42
WPl 1.....	2	2	100	0	100
XSC 1.....	5	33	0	100	100
XSC 2.....	3	17	6	94	88
XSC 3.....	2	8	0	100	100
XSC 6.....	3	22	5	95	90
XSC 8.....	6	26	27	73	46
XSC 9.....	6	23	4	96	92
XSC 10.....	5	20	25	75	50
XSC 11.....	3	15	20	80	60
XSC 12.....	3	15	20	80	60
XSC 13.....	3	14	21	79	58
XSJf 1.....	2	9	67	33	34
XSP 1.....	2	9	44	56	12
XSP 2.....	3	15	33	67	34

The answer to the first part of the first question (p. 205) is, then, "No, the branches within a single tree do not necessarily correspond with each other." To what extent there is a correspondence may be observed from the sixth column in table 157.

Question (2) on page 205 reads: "Does the amount of correspondence vary from tree to tree under the same general environment?" This question can be investigated intraspecifically and interspecifically. If one groups the various species (as from table 157), he sees at once that the range of agreement is narrowed considerably. Examples of

TABLE 158.—*Average agreement among the branches of trees in different species.*
Derived from table 157

Species	Number of trees	Number of branches Σ(a)	Σ(b). (e)	Σ(b)	Σ(b). (c)	
					Σ(b) %	
Con P	1	2	0	2	0	low
Con T	2	34	1332	74	18	low
MP	1	2	300	3	100	high
SA	2	6	204	32	6	low
TTAp	2	8	1600	16	100	high
TTC	9	81	13200	229	58	med.
TTCw	1	6	200	10	20	low
TTJ	2	18	2124	53	40	med.
TTL	2	8	900	11	82	high
TTM	2	12	684	23	30	med.-low
TTP	5	101	6502	264	25	low
WAp	1	2	102	3	34	med.
WCh, WPe, WPl..	4	14	1294	17	76	high
XSC	10	39	14500	193	75	high
XSJf	2	3	606	14	43	med.
XSP	2	5	618	24	26	low

the range of agreement are: Arizona cypresses, TTC, 44 to 100 per cent; junipers, TTJ, 38 to 60; honeylocusts, TTL, 60 to 100; apple, TTAp, no variation; maples, TTM, zero to 36; pines, TTP, 4 to 52; Arizona cypresses, XSC, 46 to 100; and pines, XSP, 12 to 34.

In spite of this lessened range, trees of the same species in the same general habitat do vary among themselves in the amount of agreement among their branches.

Table 158, which is derived from table 157, sets forth the average agreement among the branches of the trees in different species (column 6). A percentage of 0 to 30 may be classified as low average agreement, 31 to 70 as medium, and 71 to 100 as high. Thus, the gymnosperms may be grouped in order, low: Con P, Con T, TTP, and XSP; medium: TTJ, XSJf, and TTC; high: XSC and MP.

The angiosperms may be grouped in order, low: SA, TTCw, and TTM; medium: WAp; high: WCh, WPe, WPl, TTL, and TTAp. In general, the pines have a low percentage of agreement among their branches whereas the Arizona cypresses are inclined to a high percentage and yet they grow in essentially the same environment. The hardwoods from the same general locality vary in agreement from 6 to 100 percent. Those trees from the vicinity of Washington, D.C., are intermediate between the above extremes.

Insofar as present material is concerned, the generalized differences among species appear to outweigh the differences from tree to tree within a species. There remain, however, many differences between trees of the same species growing near each other which could well be ascribed to microsite factors or to individual growth form. One is inclined to correlate the disagreement among branches with the extreme forest-border conditions, and this may be legitimate. But the case of the Washington trees makes investigation under other conditions necessary.

Our third question (p. 205) reads: "Is there a similarity among branches according to the year?" In other words, is there a tendency toward unity or multiplicity of the annual increments during certain years? Because of the forest-border conditions, perhaps a better phrasing of the question is: "Are there certain years with a tendency away from the multiplicity now known to be typical of such an environment?"

Table 159 gives the ratio of single to multiple branches in actual numbers as well as pure ratio. It also gives the number of each type of branch for those species with branches sufficiently numerous to have significance (small numbers in left-hand boxes = total number of branches involved).

The most striking fact apparent at once is the great tendency toward multiplicity in all years, a fact also emphasized by previous tables. Of all years with a significant number of branches in the calculations, 1940 has the highest ratio of multiple branches—1 single to 7.4 multiple. Other years with a high ratio of multiplicity are 1935, 1936, and 1944. The years 1938, 1939, and 1942 have moderate ratios whereas 1937, 1941, 1943, and 1945 have low ratios, considering the over-all tendency toward multiplicity. The lowest ratio of the series of years is 1945, with 1 single to 0.6 multiple. If these ratios are plotted, it will be seen that there is a slight degree of repetition every 4 years and the very slightest suggestion of a repetition at about 10 years. Because of the great variations year to year (table 159), regardless of species, it seems clear that they are due to variations in habitat factors.

The lower part of table 159 sets forth the branch relations for those species from which a large number of branches was taken. No species has significant divergence from the average of all branches except TTP. Here the highest ratio occurs not in 1940, but in 1937, which in all other branches had a comparatively low ratio. If TTP were subtracted from the general average of all branches, the ratio of the latter would drop much lower. There is outright disagreement between TTP and all other branches in four years. The lowest ratios in TTP occur in 1938 and 1945. If values of TTP be eliminated from the averages of all branches, the former high and medium values will be enhanced and the low values decreased.

Insofar as the extent of the materials permits, table 159 shows clearly that there is a marked difference among the years of record in the incidence of multiplicity in branches. Further, certain years have a high incidence of multiplicity whereas others have low incidence.

The fourth and last question, asked at the start of the present section, "What is the influence of the environment?" has been answered to some extent in passing. In the extreme lower forest border, there prevails a persistent tendency toward multiplicity of growth layers in the branches, not only with respect to intra-annuals that are sharp, complete, entire, but also with respect to numerous partial growth layers such as lenses, half-lenses, and arcs. This generalized influence of the environment is undoubtedly of primary importance. The influence of different species, variation of local site factors from tree to tree, and possibly the individual growth habits of a tree constitute the factors of secondary influence. Nonetheless, they are of great importance to a study of growth layers, not only in connection with details of classification and occurrence but also in connection with the general relationship between growth layers and climate.

RELATIONS AMONG TREES OF THE SAME SPECIES

Table 157 (p. 219) gave the flush agreement for the various trees of the several species and was discussed on pages 215-220. On the whole, the relations among trees of the same species seem to be more intimate than among individual trees of different species, although this does not mean a lack of striking variation within a species.

From the above-mentioned table, it can be calculated that the average departure of the flush agreements within the trees of species TTC, from the species average (table 158), is 18.2 percent, whereas for TTP it is 15. These figures compare with the species averages of 58 and 25 percent, respectively. Hence, species TTC and TTP have

greater differences between them than do the trees within a species from the species average. The same applies to XSC which has an average departure of flush agreements within the separate trees of 19.6 percent in contrast with a species average of 75.

The general habitat relationships of the trees of TTC, TTP, and XSC are so identical that the differences among branches and trees must be ascribed to variations in local, or microsite, factors or, in the case of species, to specific differences. All the trees grew on the flat upland surface of the High Plains. Those of XSC were located 5 miles from TTC and TTP. The XSC trees were not over 200 yards apart whereas TTC and TTP on the College campus were within 600 yards of each other. The dominant summer rainfall comes in large part as intense local showers that vary greatly in amount within a fraction of a mile. All the evidence favors multiplicity, such as described in this report, as a dominant characteristic of a lower forest-border region where intense dry spells alternate with heavy rains during the warm season.

Steep slopes of other regions would tend to eliminate or mitigate certain types of rainfall and thus perhaps reduce somewhat the incidence of multiplicity. Differences in soil texture and differences in rainfall regime other than to produce a constantly high soil-moisture percentage would also modify the incidence of multiplicity either by increase or decrease. As a matter of fact, the Lubbock area is not alone in favoring multiplicity.

Fluctuations of soil moisture may stand high in the list of factors responsible for multiplicity but perhaps we must seek further for the reasons responsible for the distribution of partial growth layers. Nutrients, especially as triggered by water supply, may be insufficient to produce a growth layer as an entire sheath during a single intra-annual growth flush. They may be sufficient only for a flush producing a partial growth layer in certain branches or producing patches here and there on certain branches. Thus, perhaps, there is an element of "chance" as to which branch, or where on a single branch, a flush produces a partial growth layer.

The possible role of growth-promoting and growth-inhibiting substances must not be overlooked in regard to the localization of partial growth layers within a branch and to the variation of multiplicity among the branches of a tree.

Uncertainty will exist until we know exactly why a cambium is active at one place and not at another, and at one time and not at another.

RELATIONS AMONG DIFFERENT SPECIES

Differences and agreements among species are given in table 158 and are discussed on pages 220-221. Table 159 also shows how species differ from each other during certain years. Little need be added.

As table 158 shows, there are marked differences among species. The extremes of zero and 100 percent agreement among branches are not held exclusively by species represented by one tree only. Otherwise, agreement varies from 6 to 82 percent for SA and TTL. For species represented by more than two trees, agreements in percent are: TTC, 58; TTP, 25; WCh, WPe, WPl, combined, 76; and XSC, 75. The species designated TTP diverge from the other species by the greatest amount. The three Washington tree species seem to show the least divergence although they are from a decidedly different habitat. Lubbock trees hold a wealth of growth layers, many sharply bordered, whereas the Washington trees are multiple by the simple addition of a single highly diffuse intra-annual. This is not universal by any means.

EXTREMES OF MULTIPLICITY

Table 159 (p. 222) gave an idea of the years with the greatest multiplicity. In descending order, they were 1940, 1936, 1935, 1944, 1939, 1938, and 1942. Photographs and drawings illustrate multiplicity better perhaps than descriptions. Nevertheless, many examples have been given in the chapter on classification.

Here, section analyses will be summarized, included years given, and number of tip flushes added where possible, in order to give an idea not only of the extremes but also the range of multiplicity at the extreme lower forest border. Those sections used have had their growth layers dated exactly. Abbreviations are given on page 101.

CCCb 1-1-a (1937-1941)

13 gls + 2 L + L's—5 years.

CMJ 1-1 (1937-1940)

a. 4 sce + 3 gls + 1 psce + sL's + d $\frac{1}{2}$ L's—4 years.

b. 4 sce + 4 gls + 1 psce + sL's + d $\frac{1}{2}$ L's—4 years.

The 4 sce in CMJ 1-1 do *not* necessarily mark the outer borders of the years—1 sce marks 1938 and 3 sce are included in 1939-1940. The year 1937 has three less definite growth layers; they are designated simply as "gl's." In 1938 the psce was made by natural frost.

Con P 2-2 (1942-1944)

- a. 2 sce + 3 msce—3 tfs—3 years
 b. 2 sce + ddw—1 tf—1944 only.

Con T 1-4-a (1941-1942)

2 sce + 1 sL—3 tfs—2 years.

Con T 1-5-a (1941-1942)

2 sce + 1 dce—3 tfs—2 years.

The sharp lens of Con T 1-4 corresponds to the diffuse, complete, entire growth layer of Con T 1-5. In each case it is the year 1942 which has two diameter flushes and two tip flushes.

Con T 1-6-a (1940-1942)

4 sce + arcs—5 tfs—3 years.

Here, the 1940 increment has 1 sce plus several arcs for 2 tfs; 1941 has 2 sce for 2 tfs; and 1942 has 1 sce for 1 tf.

Con T 1-11-a (1940-1942)

4 sce + L's + arcs—4tfs—3 years.

The increment for 1940 has 2 sce plus diffuse arcs and lenses for 2 tfs.

Con T 1-18-a (1942)

1 gl + psg—2 tfs—1 year.

Con T 2-3-a (1938-1939)

2 sce + 2 d arcs—4 tfs—2 years.

Con T 2-6-b (1941-1943)

3 sce + 2 idw—4 tfs—2½ years.

Con T 2-9-a (1941-1943)

4 sce + 1 dce + 2 d arcs + 1 idw—5 tfs—3 years.

The increment for 1941 has 2 tfs and 2 sce.

SA 5-1-a (1934-1939)

7 sce + 1 sL—6 years.

The increment for 1936 has 2 sce.

SA 6-1-a (1934-1939)

6 sce + 1 psce + 1 dce + 2 sL + 2 s ½L + 1 s arc—6 years.

By selecting the proper radius, one could count 12 sharp contacts involving six years of growth.

TTAp 1-4-a (1938-1939)

2 sce + 2 dce + 1 s arc—3 tfs—2 years. (See table 52, p. 134.)

The increment for 1938 shows 1 sce and 2 dce for 2 tfs, whereas that for 1939 shows 1 sce for 1 tf.

TTAp 2-1-a (1938-1939)

4 sce—2 tfs—2 years.

In 1939 TTAp 2 grew an extra sce, probably because of irrigation in July.

TTAp 2-3-a (1938-1939)

2 sce + 2 psce + 1 sL + 2 dL + 1 d $\frac{1}{2}$ L—4 tfs—2 years. (See table 8, p. 102.)

TTC 1-11-a (1936-1945)

10 sce + 1 dce + 10 sL + 10 psL + 3 dL + 1 d $\frac{1}{2}$ L + 3 s arcs + 1 d arc—10 years. (See table 54, p. 136.)

Along different radii of TTC 1-11-a there are 30 sharp contacts, contacts in no way distinguishable from each other. Large amounts of branch material and many sections reveal in many cases those growth layers whose contacts break down to diffuse. However, multiplicity at the lower forest-border region, as represented at Lubbock, Tex., has a degree of incidence and variation as well as a variety of contacts, annual and intra-annual, that makes the dating of growth layers impossible in the absence of absolute methods. No method of counting, close inspection of contact, or "allowance" for supernumeraries could provide a substitute.

In TTC 1-11, the increment for 1939 has seven growth layers of which six are sharp or partially sharp; the increment for 1940 has six growth layers of which four are sharp or partially so; and the increment for 1941 has five growth layers of which four are sharp or partially so.

TTC 2-3-a (1935-1939)

8 sce + 4 sL—5 years.

The increment for the year 1937 has 3 sce and 1 sL which have been reduced to 2 sce, 27 cm. *outward* on the branch. The year 1939 has 2 sce and 2 sL which become 3 sce and 1 sL *outward*.

TTC 5-2-a (1935-1939)

7 sce + 2 sL + 2 psL + 1 dL + 1 s arc—5 years.

Here, there are nine wholly sharp contacts plus three partially sharp.

TTC 5-3-a (1935-1940)

5 sce + 6 msce + 3 sL + 2 msL + 1 dL + 1 s arc—5⁺ years.⁸

The plus sign is added because the sections were cut June 23, 1940, by which date 1 sce + 1 sL + 1 dL had been formed. At first sight it seems that there might be 1 sce for each year, but this is not true. The increment for 1936 contains 3 msce + 1 sL + 1 msL and that for 1937, 3 msce + 1 msL + 1 s arc, whereas 1938 has 2 sce only. Thus in TTC 5-3 the best developed and most sharply defined growth layers constitute neither the principal growth layers in all cases nor the outer boundaries of the annuals.

TTC 5-4-a (1933-1940)

9 sce + 4 sL + 1 dL—7⁺ years. (See table 10, p. 103.)

The sections were cut July 17, 1940, by which time 1 sce had been formed.

TTC 5-6-a (1936-1940)

7 sce + 1 msce + 1 psce + 1 sL + 2 psL + 2 s arcs + 1 inc L—4⁺ years.

The sections were cut August 17, 1940, by which time 1 sce + 1 psL + inc L had been formed. The increment for 1937 contains 2 sce + 1 msce + 1 psL + 1 s arc. On one part of the sections, over a distance of more than 90 degrees, 1937 has four sharply bordered growth layers and, with the lens included, five sharp margins.

TTC 5-8-a (1936-1940)

7 sce + 1 psce + 7 sL + 1 psL + 1 s arc + psg—5 years.

The sections were cut September 28, 1940, and by that time of year 1 sce + 2 sL + psg had been formed. No doubt the psg is actual post-seasonal growth. It decreases outward on the branch. With 2 sce + 3 sL, 1937 has five sharp growth layers on certain radii. With 1 sce + 1 psce + 1 psL + 1 s arc, 1938 has three sharp growth layers on certain radii. Even if all partially sharp growth layers be neglected as

⁸ A plus sign (+) after the number of years means that a branch was cut off before the end of the growing season which therefore is not recorded as a full year.

well as the seven sharp lenses, 7 sce remain to represent five years of dated growth.

TTC 5-9 (table 15, p. 104) was sectioned November 9, 1940; TTC 5-10 (table 16, p. 104), February 1, 1941; TTC 5-11 (table 160, below), April 5, 1941; and TTC 5-12 (table 17, p. 104), May 24, 1941.

TABLE 160.—TTC 5-11

	54 cm.	32 cm.
1936	2 sce	
1937	3 sce	
	1 psL	
1938	1 sce	2 sce
	1 psce	1 psce
	2 sL	1 sL (the 1 sL is more like ddw)
1939	1 sce	2 sce
	2 sL	1 sL
1940	1 sce	1 sce
	1 sL	1 sL
	2 sL	2 L (lenses fade outward)
1941	inc L	inc L

Condensed summaries of the four branches are:

TTC 5-9-a (69 cm.)

5 sce + 1 msce + 2 sL + psG—5 years.

TTC 5-10-a (53 cm.)

5 sce + 1 msce + 2 sL + 1 msL + 2 psL + 1 dL + 1 s arc—5 years.

TTC 5-11-a (54 cm.)

8 sce + 1 psce + 7 sL + 1 psL + inc—5⁺ years.

TTC 5-12-a (56 cm.)

6 sce + 3 sL + inc—3½⁺ years.

The high degree of multiplicity in the preceding tables and summaries is too strikingly obvious to require further comment.

Momentarily, attention may be directed elsewhere. First, note should be made of the longitudinal change in the content of the annual increments. Some become more complex inward, some more complex outward on the branches in the matter of sharp growth layers which can in no way at present, even under the microscope, be distinguished one from the other as to annual or intra-annual character. Multiplicity

is apparently no more characteristic of one part of a branch than of another.

Second, attention is directed to the complexity in the display of growth layers—the mixture of entire and partial growth layers; of sharp, mostly sharp, partly sharp, and diffuse; and the merging of one type into another. If, occasionally, one encounters a situation such as 1938 in TTC 5-9-a (1 sce + 1 sL), he would have little or no reason to suspect that the sharp lens does not represent an annual increment unless the growth layers are dated absolutely. The matter would be viewed differently, no doubt, in regard to 1937 of the same branch (1 sce + 1 msce). Suppose one were to study half the circuit and find two fully developed, sharply bordered growth layers; he would have no choice but to call them annual. Suppose now that the remainder of the circuit should later become available and thus reveal on the margin of one of the growth layers a breakdown to diffuseness. Would that indicate the growth layer to be intra-annual, or would it indicate that the margin of an annual can be diffuse? The further discovery of situations such as 1937, TTC 5-10-a (1 sce + 1 msce + 1 sL), and 1939 (1 sce + 1 sL + 1 psL), for instance, would convince the student that many growth layers are not to be assumed to be annual unless accurately dated.

All this series of complex growth layers is visible on stained sections under the microscope. On unstained sections, under a hand lens, the weak, highly diffuse growth layers no doubt become invisible, and the strong but diffuse-margined intra-annuals identify themselves. But what is to be done about sharp, complete, entire growth layers, and about sharp lenses and other partial growth layers? One of two courses is open: first, the application of methods of absolute dating which are restricted in scope or, second, an intensive investigation of tree growth over a number of years in a given locality and of the growth factors which promote that growth in order to make an intelligent estimate of the number of intra-annuals per century.

The complete story of a tree's response to its environment is recorded in the *entire* body of the tree and in *all* the growth layers wherever they may be, whatever their extent, and whatever their definition.

Branch TTC 12-9 (table 18, p. 105) was cut off February 29, 1940. Its summary for sections *a* (inner) reads:

13 sce + 6 psce + 3 dce + 3 sL + 1 d arc—8 years.

Some radii show many more sharply bordered growth layers than there are annual increments.

Branch TTC 12-10 (table 19, p. 105) was cut off April 21, 1940. Its summary for sections *a* (66 cm.) reads:

3 sce + 1 msce + 2 psce + 4 dce + inc L's—3⁺ years.

As the table shows, there is not *one* sce for each year. The growth for 1940 in sections *a* consists of one long and two short incomplete lenses, whereas in *b* (34.5 cm.) it is entire but incomplete, around the circuit. In most cases where branches have been cut off before the first growth layer of the season has been completed, we have found that the cambium apparently begins to divide initially at one or several points, spreading so as to create lenses which finally unite to form an entire growth layer. This appears to be true transversely as well as longitudinally.

Branch TTC 12-11 (table 161) was cut off June 29, 1940.

TABLE 161.—TTC 12-11

	65 cm.
1932	1 sce
1933	2 sce 2 psce 2 dce
1934	2 sce 1 sL 1 d arc ddw
1935	3 sce 1 sL
1936	1 sce 1 msce
1937	2 sce 1 sL 1 dL
1938	2 sce 1 psL 1 d $\frac{1}{2}$ L
1939	1 sce
1940	1 sce psg

The summary for branch TTC 12-11 reads:

15 sce + 1 msce + 2 psce + 2 dce + 3 sL + 1 psL + 1 dL + 1 d $\frac{1}{2}$ L + 1 d arc + 1 ddw + psg—8⁺ years.

In the 1935 increment the densewood of the middle growth layer breaks apart into a 120° lens whose margins are sharp, especially under high power. Under low power the nature of the lens causes two-thirds of its inner margin to appear somewhat indefinite. Further in connection with 1935, relative thicknesses do not remain the same around the circuit because the middle growth layer is thicker than the inner growth layer on one radius but considerably thinner than the inner one on the opposite radius.

The lightwood of outer 1936 disappears at two places around the circuit so that for a distance of 70° two bands of densewood lie next to each other.

The sharp lens of 1937 lies between the 2 sce and extends away from the short radius for more than half the circuit.

The outer sce of 1938 is of considerable interest because over part of the circuit its thickness is very slight and its densewood "thin" and indefinite compared with the inner sce. The densewood of the outer is itself thin and all its characteristics are subdued. Elsewhere on the circuit the contacts of the 2 sce are of equal definiteness. If it were not for the positions of the 1938 and 1939 natural frost injuries, the outer margin of 1938 would not be placed at the outer edge of the "thin" exterior growth layer—the "thin" growth layer would be included within 1939.

Branch TTC 12-12 (table 162) was cut off July 31, 1944.

TABLE 162.—TTC 12-12

	22.8 cm.	14.3 cm.	9 cm.
1942	1 sce 1 dL		
1943	2 sce	3 sce 1 sL	1 sce (outer 1943)
1944	2 sce	2 sce 1 sL	2 sce
	psg	psg	psg

A summary of sections *a* (22.8 cm.) reads:

5 sce + 1 dL + psg—3 years.

In sections *a*, the densewood of 1942 consists of two bands separated for more than half the circuit by the insertion of one to two rows of wider cells which yield the appearance of a rather indefinite lens. Without certain dating, one would be unable to classify the lens as a distinct growth layer or as an indefinite intra-annual.

The inner sce of 1943 has a margin as sharp as, or sharper than, that of the outer sce except on the short radius where, for 10° to 15° , the outer contact of the inner sce is slightly less definite than that of the outer sce. Even then it is not sufficiently indefinite to establish the inner sce as intraseasonal without other means of accurate dating.

In sections *b* (14.3 cm.), the outer margins of the 3 sce are equally sharp. However, the densewood of the middle sce is so slightly developed that it appears "thin" and less definite than the densewoods of the other 2 sce.

In sections *c* (9 cm.), the outer contacts of 1943 and of the two growth layers of 1944 are rather indefinite over an arc of about 90° .

The psg of sections *a* is a mere hint of added growth; of sections *b* it consists of several incomplete lenses one cell thick; and of sections *c* it consists merely of discrete cells scattered around the circuit.

Branch TTC 33-6 (table 163) was cut off July 31, 1944.

TABLE 163.—TTC 33-6

	18 cm.	12.5 cm.	6.5 cm.
1942	1 sce 1 dce	1 sce	
1943	1 sce 1 psce	1 sce 1 msce	1 sce
1944	2 psce	1 msce 1 psce	1 sce 1 msce 1 s arc
	inc	inc	inc L

On the long radius, for an arc of 45° , the densewood of 1943 in sections *a* (18 cm.) consists of a mere stringer made up of one or two rows of narrow cells. Three different radii on sections at 18 cm. give the following sequences with equivalent growth layers along the horizontal directions (table 164).

TABLE 164.—TTC 33-6 (18 cm.)

	Radius 1	2	3
1942	1 sce	1 sce	1 sce
1943	1 sce 1 sce	1 sce 1 dce	1 sce 1 dce (faint)
1944	1 psce 1 psce inc	1 dce 1 sce inc	1 sce 1 dce inc

On each radius of TTC 33-6 (table 164) three growth layers, but not the same three, are sharp. It is quite clear that in a lower forest-border region at least an entire section is necessary to obtain an idea of the variations among growth layers. The reading and interpretation of some sections may even present great difficulties because of the constant contrasts among different radii.

Branch TTC 33-10 (table 165) was cut off January 1, 1943.

TABLE 165.—TTC 33-10

	50 cm.	37.5 cm.	24.5 cm.
1938	1 sce		
1939	2 sce 1 psce 1 sL	1 sce	
1940	1 sce 1 psce	2 sce	
1941	1 sce 1 psce	1 sce 1 dL	1 sce 1 psL
1942	2 sce 1 sL	3 sce 1 dL	1 sce 1 psce 1 s $\frac{1}{2}$ L

A summary of sections *a*, at 50 cm., reads:

7 sce + 3 psce + 2 sL—5 years.

Without absolute dating, one would not only be confused by the different sequences on different radii, but also he would be helpless to date the growth layers because of the multiplicity involved. On four radii, 90° apart, there are 9, 10, 7, and 9 sharp growth layers. Nine sharp growth layers (7 sce + 2 sL) in five years indicate that a sharply bounded growth layer does not necessarily mark the end of a growing season.

In tree TTC 33 most intra-annuals become sharper inward on the branches.

TTC 33-11-a (1938-1942)

7 sce + 1 s arc + 2 ddw—5 years.

Both 1939 and 1942 have 2 sce.

TTC 33-12-a (1939-1942)

6 sce + 1 psL + 1 dL + 3 ddw—4 years.

The increments for 1939 and 1942 have 2 sce each.

TTC 33-13-a (1938-1942)

7 sce + 1 dce + 5 sL + 1 dL—5 years.

Here, 12 sharply bounded growth layers represent five years.

Branch TTC 33-16 (table 166) was cut off July 31, 1944.

TABLE 166.—*TTC 33-16*

	12.2 cm.	7.8 cm.
1943	1 sce	1 sce
1944	2 msce inc	2 sce inc

Tip growth measurements on TTC 33-16 were made on January 30, 1943, January 22, 1944, and July 31, 1944; the sections were cut from the tip growth of 1943. Hence, this branch is an example of measured multiplicity. Note should be made of the amount of diameter growth which had taken place *before* July 31, 1944. At 12.2 cm. the cambium appeared to be active, whereas at 7.8 cm. it had become inactive.

The history and observation of branch TTC 33-20 (table 167) were identical with those of TTC 33-16.

TABLE 167.—*TTC 33-20*

	13.4 cm.	7.8 cm.
1943	1 sce 1 d arc	1 sce
1944	2 sce inc	2 sce inc

The "inc" had practically completed its growth. The formation of 3 sce by July 31 shows that the time of rapid xylem formation comes during the first half of the warm season.

TTC 34-2 (1936-1941)

a. 9 sce + 1 msce + 2 sL + 3 dL + 1 d arc + psg—6 years.

b. 6 sce + 2 psce + 6 sL + 1 dL + 1 s $\frac{1}{2}$ L + psg—5 years.

Branch TTC 34-2 was dead at the time of cutting, November 29, 1941, its cambium having been killed by artificial freezing on May 18, 1941. The presence of psg indicates that the cambium was active when killed. To give an idea of the amount of growth that had oc-

curred prior to the death of the cambium, the following display of 1941 is given.

TABLE 168.—*TTC 34-2*

	50 cm.	40 cm.	30 cm.
1941	3 sce	1 sce	2 sce
	1 dL	2 sL	2 sL
	psg	psg	psg (inc L)

In tree *TTC 34*, the increment for the year 1940 commonly has 2 sce.

TTC 35-7-a (1943-1944)

4 sce + 1 psce + inc—1⁺ years.

For the year 1944, sections *a* of *TTC 35-7* contained 3 sce+inc. Nine cm. outward on the branch the 3 sce become 3 dce. The branch was cut off July 31, 1944.

TTC 36-1-a (1938-1942)

6 sce + 1 sL + 1 s $\frac{1}{2}$ L + 1 d $\frac{1}{2}$ L + 2 ddw—5 years. (See table 28, p. 107, for part of *TTC 36-1*.)

TABLE 169.—*TTC 36-3*

	58.5 cm.	47.5 cm.	34.5 cm.
1938	1 sce		
1939	1 msce	1 sce	
1940	1 sce 1 psce	1 sce	1 sce
1941	1 msce 1 dL	1 sce 1 sL	1 sce
1942	1 sce 2 psce ddw psg	1 sce 2 dce (faint)	1 sce

Definition of growth layer decreases inward on the branch, *TTC 36-3* (table 169), in four cases in contrast with one case of increase. Also, complexity increases inward.

TTC 36-5-a (1938-1942)

6 sce + 2 msce + 3 psce + 1 dce—5 years. (See table 29, p. 107, for part of *TTC 36-5*.)

TTC 36-6-a (1937-1942)

7 sce + 1 psce + 1 sL + 2 psL + 2 dL + 1 d arc + 2 ddw—6 years.

TTC 36-7-a (1938-1942)

4 sce + 1 msce + 2 psce + 2 sL + 1 psL + 1 d $\frac{1}{2}$ L + 1 ddw—5 years.

The increment for 1938 consists of 1 msce and 1 psce.

TTJ 2-4-a (1937-1942)

7 sce + 2 dce + 2 dL + 1 s arc—6 years.

TTJ 2-5-a (1938-1942)

6 sce + 1 dL—5 years.

The increment for 1940 has 2 sce which becomes less sharp outward on the branch. In sections *a* at 48.5 cm. from the tip, the densewood of the inner growth layer of 1940 is much heavier than the densewood of the outer growth layer; at 36 cm., the inner densewood is less sharp; and at 25 cm., it has nearly disappeared.

TTP 20-1-a (1935-1939)

5 sce + 1 msce + 1 dce + 1 sL + 2 psL + 1 d arc—5 years.

In TTP 20-1-a the partly sharp lenses appear to be completely sharp under very low powers.

TTP 20-2-a (1937-1939)

4 sce + 1 dce + 3 dL—3 years.

The increment for 1937 possesses 2 sce + 2 dL.

TTP 20-4-a (1936-1939)

4 msce + 1 psce + 2 sL + 2 msL + 1 dL + 1 pcL—5 tfs—4 years.

The increments for 1936, 1937, and 1938 are terminated by growth layers not completely sharp.

TTP 20-11-a (1940-1941)

2 sce + 1 msce + 1 dce—2 tfs—2 years.

TTP 20-13-a (1940-1941)

2 sce + 1 psce + 1 dce—2 tfs—2 years.

TTP 20-16-a (1942-1944)

3 sce + 1 dce + 2 sL + 1 dL—4 tfs—3 years.

Two tip flushes are not recorded by sharp growth layers in 1942 (1 sce + 1 dce), but two annual tip flushes correspond to four sharp diameter flushes in 1943 and 1944 (1 sce + 1 sL and 1 sce + 1 sL + 1 dL).

TTP 20-18-a (1940-1942)

3 sce + 2 dce—3 tfs—3 years.

TTP 20-23-a (1943-1944)

3 sce + inc—2 tfs—2 years.

Tip growth of TTP 20-23 was measured January 30, 1943, February 5, 1944, and November 14, 1944. For each year included, 1943 and 1944, one tip flush was formed. In the 1943 increment, one diameter flush was made and in 1944, two diameter flushes. This is measured multiplicity, not only in sections *a* taken from the 1943 tip growth, but also in sections *b* taken from 1944 tip growth. Two diameter flushes correspond to one tip flush. In TTP 20-25, also with measured tip flushes, two diameter flushes correspond to two tip flushes.

TTP 20-25-a (1943-1944)

3 sce—3 tfs—2 years. (See table 75, p. 145.)

TTP 20-27-a (1943-1944)

2 sce + 1 dce—3 tfs—2 years. (See table 76, p. 146.)

TTP 20-33-a (1943-1944)

2 sce + 1 dce + ddw—3 tfs—2 years.

TTP 20-34-a (1943-1944)

2 sce + 1 dce + 1 dL + 1 d arc—3 tfs—2 years.

TTP 20-36-a (1943-1944)

2 sce + 1 psce + 1 dce—3 tfs—2 years. (See table 81, p. 149.)

The branches of TTP 20 illustrate the variety to be found among growth layers, tip flushes, and diameter flushes.

TTP 21-1-a (1936-1940)

5 sce + 1 msce + 1 psce + 1 inc L—6 tfs—4* years.

The increments for the years 1936 and 1937 have 2 sce each whereas 1939 has 1 msce and 1940 has 1 psce + inc L.

TTP 21-2-a (1937-1940)

6 sce + 1 dgl + 1 dL + arcs—5 tfs—3* years.

Branch TTP 21-2 was cut off July 17, 1940, by which time it had grown 1 sce + 1 dgl. The diffuse growth layer, which is interior to the sce, shows scattered radial columns of cells whose outer members remain narrow as in typical densewood. In 1937, 3 sce are present.

TTP 21-3-a (1936-1940)

7 sce + 1 sL—5 tfs—5 years.

The increments for 1936 and 1937 each contain 2 sce.

TTP 21-6-a (1935-1940)

7 sce + 1 dce—6 tfs—6 years.

The dce represents 1938. Both 1936 and 1937 have 2 sce each.

TTP 21-8-a (1936-1940)

5 sce + 1 msce + 1 psce + 1 d arc—5 tfs—5 years. (See table 86, p. 151.)

The 1 msce represents 1938, and the 1 psce represents 1939. Both of these become sharp 26 cm. outward on the branch. Again 1936 and 1937 are represented by 2 sce each.

TTP 21-10-a (1936-1940)

5 sce + 2 dce—7 tfs—5 years.

The 2 dce represent 1939 and 1940. Both 1936 and 1937 have 2 sce each. Therefore seven diameter flushes correspond to seven tip flushes put down in five years.

TTP 22-2-a (1940-1941)

2 sce + 1 psce + 1 dce—2 tfs—2 years.

Here, the intra-annual growth layers, 1 psce and 1 dce, do not correspond to tip flushes.

TTP 24-3-a (1935-1941)

5 sce + 3 msce + 2 dce + 1 pcL—7 years. (See table 92, p. 156.)

The growth layers designated 3 msce represent 1939, 1940, and 1941; 1 dce represents 1938. In the 1941 increment, the lightwood of the msce is lenticular, the densewood being continuous around the circuit. When high power was used on what had been interpreted as a lens, it was revealed that the lightwood only, and not the densewood, is lenticular. Thus the question again arises: "Does a lens ever represent an annual increment?" This naturally creates the further ques-

tion, "Can a large portion of the cambium of a tree remain inactive (i.e., in that condition intermediate between death and active cambial division) from the end of one growing season to the start of the second one hence?"

TTP 24-14-a (1937-1942)

6 sce + 1 psce + 1 dce + 1 sL + ddw + psg—6 tfs—6 years.

TTS 1-1-a (1936-1939)

6 sce + sL's + s $\frac{1}{2}$ L's + s arcs + arcs—4 tfs—4 years.

WAp 1-1-a (1943-1944)

2 sce + 1 sL—2 tfs—2 years.

WAp 1-3-a (1943-1944)

2 sce + 1 dce—3 tfs—2 years.

Here 1944 is composed of 1 dce + 1 sce, each corresponding to a tf.

WCh 2-6-a (1944-1945)

2 sce + 2 dce—3 tfs—1⁺ years. (See table 99, p. 160.)

Branch WCh 2-6 was cut off June 17, 1945, by which time in 1945, 1 sce had been formed 45.8 cm. in from tip, and 1 sce + 1 dce had been formed 28.7 cm. in from tip. These corresponded to 1 tf. In contrast, 1944, 45.8 cm. from tip, had 1 sce + 2 dce, the 3 dfs to correspond to 2 tfs.

WPe 1-4-a (1943-1944)

2 sce + 1 psce—4 tfs—2 years.

Branch WPe 1-4 was cut off January 21, 1945. Detailed analysis is given in table 170.

TABLE 170.—*WPe 1-4*

	38.5 cm.	33 cm.	23.5 cm.	7.5 cm.	TF
1943	1 sce				1
1944	1 sce	1 sce	1 sce	1 sce	1
	1 psce	1 psce	1 psce		2

Sections at 38.5 cm. in WPe 1-4 (table 170) came from the latest 1943 tip growth and therefore could have only 1 sce for 1 tf. Growth for 1944 contained 3 tfs, the second and third a direct continuation of the first. Sections at 33 cm. came from the first tf; at 23.5 cm. from

the second tf; and at 7.5 from the third tf. Hence, the 1 psce corresponds to the first two tfs and the 1 sce to the third tf.

TABLE 171.—*WPe 1-5*

	8.5 cm.	22.5 cm.	TF
1944	1 sce	1 sce	1
	1 psce		
1945	inc (p)	inc (p)	1

Branch *WPe 1-5* (table 171) was cut off June 17, 1945. It had grown a "first flush" of 11 cm. after which its original tip had died. Sections at 8.5 cm. were taken 8.5 cm. inward from the dead tip. The "second" tip flush was a branch coming off the first tip flush 3 cm. back from the dead tip—it began growth after the original tip had died. Tip growth for 1945 was a linear addition to second 1944. Sections at 22.5 cm. came from 4 cm. outward in second 1944—the lateral branch. The 1 psce corresponds to the first tip flush, the one with the dead tip; the 1 sce corresponds to the second tip flush, the lateral branch. Hence, nonlinear tip flushes, as well as linear, can have diameter flushes corresponding to them. The growth layer for 1945 was nearly, if not quite, complete.

TABLE 172.—*WPe 1-6*

	24 cm.	19 cm.	37 cm.	TF
1943	1 sce			1
	1 psce			1
1944	1 sce	1 sce	1 sce	1
	1 psce	1 psce		1
1945	inc	inc	inc	1

Branch *WPe 1-6* (table 172) was cut off June 17, 1945, after a tip growth of 14.5 cm. which was a linear continuation of the second 1944 tip flush. The second 1943 tip flush of 2 cm. was a direct linear continuation of the first 1943 tip flush; sections at 24 cm. came from 3 cm. inward from the outer end of first 1943. The first 1944 tip flush was a linear continuation of 1943, retaining a length of 19 cm. after its tip had died; sections at 19 cm. came from a very slight distance out from the start of first 1944. Second 1944 tip growth came out as a lateral (or nonlinear) branch back from the dead tip and attained a length of 24.5 cm.; sections at 37 cm. came from 2 cm. out from the base of the second 1944 tip flush. Hence, 1943 with two "linear" tip flushes contains a growth layer for each, and 1944 with two "non-

linear" tip flushes also contains a growth layer for each. There is very little difference among the outer boundaries of the increments for 1943, 1944, and 1945, whether annual or intra-annual. The chief difference lies in vessel size and number, and this difference is only of local use.

Branch XSC 1-1 (table 42, p. 110) was cut off May 10, 1940, after having been frozen April 8, 1940, at 81 cm. A summary of sections *a* at 81 cm. follows.

13 sce + 1 msce + 2 psce + 2 sL + 5 psL + 1 dL + 1 s $\frac{1}{2}$ L + 2 $\frac{1}{2}$ L + 1 ddw + inc—8* years.

XSC 1-2 (1932-1940)

- a. 13 sce + 2 msce + 1 psce + 7 sL + 2 msL + 2 psL + dL's + 3 s $\frac{1}{2}$ L + 2 d $\frac{1}{2}$ L + 1 d arc + 1 ddw + inc L—8* years. (See table 102, p. 162.)
- b. 17 sce + 1 psce + 10 sL + 1 msL + 3 psL + 2 dL + 2 s $\frac{1}{2}$ L + 5 d $\frac{1}{2}$ L + 1 d arc + 1 s ddw + 3 ddw + inc—8* years.

Branch XSC 1-2 was cut off May 10, 1940. Both XSC 1-1 and 1-2 were frozen artificially on April 8, 1940, the latter more than twice as long. The effect of freezing in XSC 1-2 was much more severe, the initiation of recovery apparently delayed, and the amount of recovery much less in the time between freezing and cutting off the branch. At the time of freezing of XSC 1-2, only scattered lenses of one or two rows of cells had been formed, and by the time of cutting, one to six rows of recovery cells had been added.

XSC 1-3-a (1936-1939)

8 sce + 7 sL—4 years.

The cambium had not yet become active by April 9, 1940, when branch XSC 1-3 was cut off. If we include the years 1930 to 1935, which do not appear in the summary above, we obtain:

18 sce + 2 msce + 11 sL + 1 dL—10 years.

The multiplicity in sections *b* is without doubt even greater. In fact, on one radius, there are 27 sharp growth layers for nine years. Other radii give other combinations, not duplicating the first radius.

XSC 1-4-a (1933-1940)

9 sce + 1 msce + 10 sL + 1 msL + 3 dL + 2 ddw + inc—7* years.

If the 3 years prior to 1933 are included, we must add 7 sce, 1 psce, and 1 dce. Therefore, the years 1933-1939 include 19 sharp growth layers, representing 7 years, and the interval 1930-1939 includes 26 sharp growth layers for 10 years.

XSC 1-5-a (1936-1940)

2 sce + 1 msce + 8 sL + 3 psL + 1 dL + 1 s $\frac{1}{2}$ L + ddw—5 years. (See table 103, p. 165.)

If we include 1930 to 1935, we must add 16 sce + 3 sL + 1 dL + 1 ddw.

Tree XSC 1 has a high degree of multiplicity, parts of which may be exaggerated because of irrigation during 1936 and prior years. Nonetheless, a rather high degree of multiplicity characterizes the lower forest-border zone, accentuated downward or toward the drier areas and diminished upward or toward the wetter areas. This fact of multiple growth in an extreme lower forest-border situation, combined with methods of absolute dating, make the Lubbock region nearly ideal for learning what a tree can and will do in response to highly variable growth factors.

Two additional comments are suggested. First, nearly all of our specimens are from branches. The evidence we do have, added to the tracing of growth layers inward on the branches, indicates that the trunks participate in multiplicity. If, in some cases, the record in the trunks is subdued, in comparison with that in the branches, then the branches are giving a more complete and more detailed ecologic story.

Second, without methods of absolute dating, the complexity of the sections would make them useless for any information based on precise years. Wholly apart from this, however, the pattern formed by the complex array of partial and entire growth layers testifies eloquently to the impact of highly variable growth factors. If fluctuations of soil moisture are great and of paramount importance in a dry climate, we receive an excellent idea of the rainfall regime which recharges the supply of soil moisture.

XSC 2-1-a (1934-1940)

13 sce + 13 sL + 2 ddw + inc—6* years. (See table 104, p. 165.)

Branch XSC 2-1 was cut off May 10, 1940, after having been frozen artificially April 8, 1940. Sections *a* contain 26 sharply bordered growth layers for 6 years—it is again obvious that a sharply bordered growth layer is not necessarily annual.

XSC 2-2 (1934-1940)

a. 18 sce + 1 dce + 7 sL + 1 msL + 1 dL + arcs—6* years. (See table 105, p. 166.)

Branch XSC 2-2 was cut off May 26, 1940. Here, 25 sharp growth layers represent 6-plus years. Various radii give different combinations of sharp and diffuse growth layers.

Sections *b*, 17 cm. outward from *a*, give:

18 sce + 1 dce + 6 sL + 2 msL + 1 dL + inc—6⁺ years.

The sce are identical with those in *a*; 1 msL and the dL are different; three of the sL are different; and the dce are the same.

Sections *c*, 12 cm. outward from *b*, give:

19 sce + 1 dce + 9 sL + 1 msL + inc—6⁺ years.

The sce and the 1 dce are most closely identical in *a*, *b*, and *c*; 3 sL are new in *c* over *b* or 4 sL over *a*; and the 1 msL is totally different.

XSC 2-3-a (1934-1940)

3 sce + 12 msce + 5 sL + 1 psL + 2 ddw—6⁺ years. (See table 106, p. 166.)

Branch XSC 2-3 was cut off April 11, 1940. The years 1934 to 1937 are represented by 12 msce + 2 sL + 1 psL. Even though parts of the circuits are diffuse, the msce are, nevertheless, annual boundaries.

XSC 4-1-a (1932-1939)

14 sce + 1 dce + 12 sL + 1 msL + 1 dL + 2 arcs + 1 ct + 2 ddw—8 years.

The branch XSC 4-1 has 26 sharp growth layers, and one mostly sharp, for eight years.

XSC 6-1-a (1933-1940)

12 sce + 10 sL + 1 msL + 3 dL + 2 ddw + inc—7⁺ years.

Branch XSC 6-1 was cut off May 10, 1940, and sections *a* were taken 118 cm. from the tip. The complexity of 1935 in both sections *a* and *b* is particularly confusing because the densewood of the outer growth layer of the year is weak and "thin." It consists of one to two cell-rows. But this annual margin is no better, in some cases worse, than the outer margins of the intra-annuals of 1935 which we have called "stringers." In addition, the increment contains a thick growth layer with heavy densewood succeeded by a thin growth layer with "thin," weak densewood. This situation of an "outer thin" growth layer has, heretofore, commonly appeared as the outer border of an annual increment. In 1935 of XSC 6-1, it is simply another intra-annual.

XSC 6-2-a (1933-1939)

8 sce + 1 gl + 12 sL + 5 dL + 1 ct—7 years.

Sections XSC 6-2-a came from 117 cm. inward from the tip.

XSC 6-3-a (1933-1940)

7 sce + 2 msce + 1 dce + 8 sL + 1 msL + 4 s $\frac{1}{2}$ L + 5 ddw + 2 ct—8 years.

Both years, 1938 and 1939, are represented chiefly by 1 msce each. In the 1939 increment, much of the densewood is an irregular "stringer," a single cell thick, which lies one to two cells out from the 1938 densewood. The multiple densewood of 1938, added to the poor definition and development of 1939, creates an uncertainty which would be fatal were it not for the frosts which date the growth layer.

XSC 8-1-a (1936-1940)

6 sce + 2 msce + 1 gl + 4 sL + 1 ddw—5 years.

Sections of XSC 8-1-a show 10 sharp growth layers on certain radii and 12 on others.

XSC 8-3-a (1937-1940)

4 sce + 1 msce + 1 sL + 1 dL + 2 s arcs + 3 d arcs + 1 ddw—4 years.

Different radii on sections of branch XSC 8-3 show many different sequences because of the many sharp or partly sharp growth layers.

XSC 8-4-a (1937-1940)

5 sce + 2 msce + 1 psce + 3 sL + 1 dL + 1 s arc—4 years. (See table 112, p. 170.)

The variety of growth layers in XSC 8-4 gives many different radial counts. Sections *a* at 66.5 cm., sections *b* at 50 cm., and sections *c* at 37 cm. possess identical sequences save for 1939 of *c* which has 2 sce instead of 1, as in *a* and *b*.

XSC 9-2-a (1938-1940)

3 sce + 1 msce + 2 psce + 3 dce + 1 sL + 1 msL—3 years.

XSC 9-3-a (1938-1941)

7 sce + 1 dce + 1 sL + 1 msL + 1 dL + inc L's—3⁺ years. (See table 114, p. 171.)

Branch XSC 9-3 was cut off June 6, 1941, after having been frozen artificially on May 9, 1941. The increment for 1941 contains 1 sce + inc L's.

XSC 9-4-a (1938-1941)

7 sce + 1 dce + 1 sL + 1 msL + 1 dL + 1 ddw + inc L—3⁺ years. (See table 115, p. 171.)

Branch XSC 9-4 was cut off June 14, 1941, after having been frozen artificially on May 9, 1941. One sce plus an inc L constitutes 1941.

XSC 10-2-a (1938-1940)

3 sce + 2 psce + 1 dce + 1 sL + 2 msL + 2 psL + dw—3 years.

XSC 11-2-a (1938-1940)

2 sce + 1 msce + 2 psce + 1 dce + 1 sL + 2 dL + 1 d $\frac{1}{2}$ L + 1 ddw—3 years.

In XSC 11-2-a, the 1939 increment is terminated radially outward by the 1 msce. Poor annual contacts are by no means a rare feature.

XSC 12-1-a (1938-1940)

6 sce + 1 msce + 1 sL + 2 dL + 1 d $\frac{1}{2}$ L + 1 ddw + 1 dw—3 years. (See table 122, p. 175.)

XSC 13-1-a (1938-1940)

4 sce + 3 msce + 1 psce + 1 dce + 1 sL + 2 ddw—3 years. (See table 124, p. 177.)

Branch XSC 13-1, as summarized above, appears to have one extra sce in the three years. This is not true: 1938 has 3 msce + 1 psce + 1 sL + 1 ddw, whereas 1939 has 3 sce + 1 dce.

XSP 1-2 (1936-1940)

a. 6 sce + 1 sL + 1 ce + 1 ddw—? tf—5 years.

The ce of XSP 1-2 makes up the outer growth layer of 1940. Its densewood is feeble and intermittent because scattered radial columns of cells do not become narrow radially.

Sections *b* (1939-1940), 29 cm. outward from *a*, can be summarized as:

b. 3 sce + 1 sL + 1 ce—3 tfs—2 years.

XSP 2-1-a (1936-1939)

6 sce + 2 dL + arcs + 1 ddw—4 years. (See table 131, p. 180.)

XSP 2-2-a (1935-1939)

5 sce + 1 sL—5 years.

In XSP 2-2, 1 sce corresponds to each of the years involved. But, in this otherwise simple sequence, one sharp lens intrudes to give a single touch of multiplicity.

TABLE 173.—XSP 2-3

	44 cm.
1936.....	1 sce ddw
1937.....	1 sce
1938.....	2 sce
1939.....	2 sce
1940.....	1 sL inc

In a third branch of the same tree, XSP 2-3 (table 173), multiplicity again increases so that it summarizes as:

6 sce + 1 sL + ddw + inc—4 + years.

The branch was cut off June 12, 1940, by which time concurrent lenses and an almost complete, entire growth layer had been formed.

YCt 1-3 (1940)

a. 4 sce—1 tf—1 year.

b. 3 sce + 1 sL—1 tf—1 year.

YCt 1-6-a (1940)

3 sce—2 tfs—1⁺ year.

The branches designated YCt 1 came from the tip flush which grew during 1940, but not necessarily from the same tree. Definite evidence of growth cessation was absent although the sections were cut November 21, 1940. In fact, a majority of the sections were growing at the time they were cut.

YCt 2-1-a (1939-1940)

15 to 20 gls—2 or 2⁺ tfs—2 years.

YCt 2 includes all branches containing the growth of two years, not necessarily from the same tree. The sections 2-1-a gave a bit of trouble because of the rapid succession of zones of vessels and zones of narrow, much lignified tracheids. Clearly evident were the growth pulsations. Up to 20 entire growth layers and lenses are present in sections *a*. In *b*, the growth layers are fewer in number and more

definite. The cells just under the cambium give no indication that the date of cutting was as late as November 21. This, combined with the fact that the annual increments cannot be separated, suggests that water fluctuations cause the growth pulsations as expressed in the growth layers. In fact, the trees are known to grow after each irrigation.⁹ Tip flushes are given as 2+, 5+, and the like, in YCt 2 because the branch material available to us was cut so as to include only that part of the branch length which had grown during 1939.

YCt 2-2-a (1939-1940)

3 sce + 5 to 6 sL + psg—1 or 1⁺ tfs—2 years.

Vessel and tracheid succession is much more definite in YCt 2-2. Definite terminal bud scale scars did not exist between 1939 and 1940 growth. As before, the cutting date was November 21, 1940. Typical vessels had been formed in contact with the cambium. In fact, many of the vessels had differentiated so rapidly on the outer margin of the xylem that the cambium protruded outward over the vessels. As a manner of speaking, vessel formation in this ring-porous wood had no regard for the time of year.

YCt 2-3-a (1939-1940)

8 to 10 sce + 4 to 6 sL + psg—2 or 2⁺ tfs—2 years.

Growth was not quite so active outward on the branch, YCt 2-3, at the time of cutting, November 21, 1940.

YCt 2-4-a (1939-1940)

4 to 5 sce + 2 to 3 L's + psg—2 or 2⁺ tfs—2 years.

YCt 2-5-a (1939-1940)

6 sce + 6 L's + psg—5 or 5⁺ tfs—2 years.

Sections *a* to *e* were taken from YCt 2-5, so that *a* and *b* came from the oldest tip flush of 1939, *c* from the second, *d* from the third, and *e* from the fourth or youngest. Because we did not know how many tip flushes grew in 1940 on this branch, one or one-plus is added to the four for 1939. The important feature of YCt 2-5 is the increase in the number of sce outward, even an increase outward within the oldest tip flush of 1939 by the sudden insertion of entire growth layers and lenses. This high localization of, and rapid transition among, growth layers in the Yuma area appears to be simply an exaggeration of the

⁹ Personal communication from C. W. Van Horn, Superintendent, Yuma Farms, University of Arizona Agricultural Experiment Station.

same tendency in the Lubbock area. In sections *e*, on the long radius, a thick lens of immature cells was being laid down at the time of cutting, November 21, 1940.

Among the sce of YCt 2-5, certain growth layers stand out as more sharply set off and as containing a more nearly normal internal sequence. These correspond to the recorded tip flushes. On the whole, growth flushes and growth fluctuations in the Yuma area appear to be due not so much to temperature as to variations in water supply.

YCt 3-1-a (1938-1940)

11 to 13 sce + L's + psg—3 years.

Unfinished concurrent lenses showed active growth to have been in progress on November 21, 1940, in YCt 3-1-a.

YCt 4-1-a (1937-1940)

16 sce + many L's + psg—4 years.

YCt 4-2-a (1937-1940)

12 sce + 5 to 8 L's + psg—4 years.

The actual separation of the growth layers in YCt 4-2 has been given in table 141, page 182. If we summarize the branches of YCt, we find that, on the average, four or more growth layers were formed per year.

A wholly complete graph of true cambial activity and growth flushes, no matter how transitory the impulse and subdued the effects, or how prolonged the impulse and magnified the effects, would give the only genuine picture of the impact upon the body of the tree not only of the complex of site factors but also of the complex of microsite factors within the larger framework. At present, we can only hope for such a graph. At best, we have recorded such growth layers as sce, sL, s arc, s $\frac{1}{2}$ L, msce, msL, psce, psL, dce, dL, and the like. Diffuseness in itself varies over a wide range of definiteness and visibility. Hundreds of dce's, dL's, and d arcs have passed unmentioned and, no doubt, many more passed unnoticed. Slight evidence of a change in growth activity resides in the faintest of the diffuse growth layers. Interrupted lightwood, interrupted densewood, divided densewood, and divided lightwood also testify to a change of pace in growth activity. Therefore, the growth flushes here recorded and discussed as growth layers include those easily identified and strikingly visible. In contrast to an ultimate graph of growth variations and cambial activity, the material described herein is, in a manner of speaking, a preliminary portrayal. Nonetheless, it gives a broad hint of the

complexity of the processes involved and of the wealth of variations and their rate in time, as well as an indication of the real multiplicity of growth flushes.

A summary of growth flushes as such, is given in table 174. The number for each branch or each section is an absolute minimum. All types of growth layers are included. Insofar as a flush is concerned, a diffuse, complete, entire growth layer, a diffuse lens, or diffuse arc is just as important ecologically as a sharp, complete, entire growth layer, a sharp lens, or sharp arc. In addition to multiplicity, the table also illustrates some of the relationships between tip flushes and diameter flushes, and between tip flushes and years.

Table 175 gives chiefly the average number of diameter flushes per year per species. Entries for Con T, TTC, TTJ, TTP, and XSC are closer to a general average because of the large number of branches used. These figures came from branches which may be thought to emphasize multiplicity; nevertheless they are representative and do include branches of all types. The pines in general have a low "factor

TABLE 174.—*Total number of growth flushes for the number of years indicated*
DF = diameter flushes; TF = tip flushes.

DF	TF	Years	DF	TF	Years
CCCb 1-1-a ... 15		5	TTC 5-6-a 15		4+
CMJ 1-1-a 14+		4	TTC 5-8-a 18		5
CMJ 1-1-b 15+		4	TTC 5-9-a 9		5
Con P 2-2-a ... 5	3	3	TTC 5-9-b 8		4
Con P 2-2-b ... 3	1	1	TTC 5-10-a ... 13		5
Con T 1-4-a ... 3	3	2	TTC 5-10-b ... 10		3
Con T 1-5-a ... 3	3	2	TTC 5-11-a ... 18		5+
Con T 1-6-a ... 6+	5	3	TTC 5-11-b ... 12		3+
Con T 1-11-a .. 8+	4	3	TTC 5-12-a ... 10		3½+
Con T 1-18-a .. 2	2	1	TTC 5-12-b ... 6		3+
Con T 1-19-a .. 2	2	2	TTC 12-9-a ... 26		8
Con T 2-3-a ... 4	4	2	TTC 12-9-b ... 21		7
Con T 2-6-b ... 5	4	2½	TTC 12-10-a .. 11		3+
Con T 2-9-a ... 8	5	3	TTC 12-10-b .. 6		2½+
SA 5-1-a 8		6	TTC 12-11-a .. 29		8+
SA 6-1-a 13		6	TTC 12-12-a .. 7		3—
TTAp 1-4-a ... 5	3	2	TTC 12-12-b .. 8		2—
TTAp 2-1-a ... 4	2	2	TTC 12-12-c ... 4		1
TTAp 2-3-a ... 8	4	2	TTC 33-6-a ... 7		2+
TTC 1-11-a ... 36		10	TTC 33-6-b ... 6		1½+
TTC 2-3-a 12		5	TTC 33-6-c ... 5		1
TTC 5-2-a 13		5	TTC 33-10-a .. 12		5
TTC 5-3-a 18		5+	TTC 33-10-b .. 9		4
TTC 5-4-a 14		7+	TTC 33-10-c .. 5		2

(Continued)

TABLE 174.—*Concluded*

<i>DF</i>	<i>TF</i>	<i>Years</i>		<i>DF</i>	<i>TF</i>	<i>Years</i>
C 33-11-a .. 10		5	WPe 1-5-b	2	2	½+
C 33-12-a .. 11		4	WPe 1-6-a	5	5	2+
C 33-13-a .. 14		5	WPe 1-6-b	3	3	1+
C 33-16-a .. 4		1+	XSC 1-1-a	29		8
C 33-16-b .. 4		1+	XSC 1-1-b	31		8
C 33-20-a .. 5		1+	XSC 1-2-a	37+		8+
C 33-20-b .. 4		1	XSC 1-2-b	47		8+
C 34-2-a ... 17		6	XSC 1-3-a	15		4
C 34-2-b ... 17		5	XSC 1-3-a	32		10
C 35-7-a ... 6		1+	XSC 1-4-a	27		7+
C 36-1-a ... 11		5	XSC 1-4-a	36		10+
C 36-3-a ... 11		5	XSC 1-5-a	17		5
C 36-3-b ... 7		4	XSC 1-5-a	38		11
C 36-3-c ... 3		3	XSC 2-1-a	29		6+
C 36-5-a ... 12		5	XSC 2-2-a	30+		6+
C 36-6-a ... 16		6	XSC 2-2-b	29		6+
C 36-7-a ... 12		5	XSC 2-2-c	31		6+
J 2-4-a 12		6	XSC 2-3-a	23		6+
J 2-5-a 7		5	XSC 4-1-a	34		8
P 20-1-a ... 11		5	XSC 6-1-a	29		7+
P 20-2-a ... 8		3	XSC 6-2-a	27		7
P 20-4-a ... 11	5	4	XSC 6-3-a	30		8
P 20-11-a .. 4	2	2	XSC 8-1-a	14		5
P 20-13-a .. 4	2	2	XSC 8-3-a	13		4
			XSC 8-4-a	12		4
P 20-16-a .. 7	4	3	XSC 9-2-a	11		3
P 20-18-a .. 5	3	3	XSC 9-3-a	11		3+
P 20-23-a .. 4	2	2	XSC 9-4-a	12		3+
P 20-25-a .. 3	3	2	XSC 10-2-a ...	12		3
P 20-27-a .. 3	3	2	XSC 11-2-a ...	11		3
P 20-33-a .. 4	3	2	XSC 12-1-a ...	13		3
P 20-34-a .. 5	3	2	XSC 13-1-a ...	12		3
P 20-36-a .. 4	3	2	XSP 1-2-a	8		5
P 21-1-a .. 8	6	4+	XSP 1-2-b	5	3	2
P 21-2-a .. 10	5	3+	XSP 2-1-a	11+		4
P 21-3-a .. 8	5	5	XSP 2-2-a	6		5
P 21-6-a .. 8	6	6	XSP 2-3-a	9		4+
P 21-8-a ... 8	5	5	YCt 1-2-a	2	1	1
P 21-10-a ... 7	7	5	YCt 1-3-a	4	1	1
P 22-2-a ... 4	2	2	YCt 1-3-b	4	1	1
P 24-3-a ... 11		7	YCt 1-6-a	3	2	1—
P 24-14-a .. 11	6	6	YCt 2-1-a	15 to 20	2 or 2+	2
S 1-1-a 14+	4	4	YCt 2-2-a	9 to 10	1 or 1+	2
p 1-1-a 3	2	2	YCt 2-3-a	13 to 17	2 or 2+	2
p 1-3-a 3	3	2	YCt 2-4-a	7 to 9	2 or 2+	2
h 2-6-a ... 4	3	1+	YCt 2-5-a	13	5 or 5+	2
e 1-4-a 3	4	2	YCt 3-1-a	14 to 16		3
e 1-4-b 2	3	1	YCt 4-1-a	21+		4
e 1-5-a 3	3	1+	YCt 4-2-a	18 to 21		4

of multiplicity" whereas the Arizona cypresses have a high factor, both in their way testifying to the conditions existing in the extreme lower forest-border region.

Although the figures of table 175 could be made more precise, they are significant, and they indicate the "factor of multiplicity" for the region. Only extended measurement and observation can reveal the "factor of multiplicity."

A summary of extremes of multiplicity may be brought together. (1) Multiplicity exists. (2) All classes and types of growth layers are

TABLE 175.—Average number of diameter and tip flushes per year per species

	DF	TF
CCCb	3	
CMJ	3.9	
Con P	2	1
Con T	2.1	1.6
SA	1.75	
TTAp	2.75	1.5
TTC	3.03	
TTJ	1.7	
TTP	1.8	1.05
TTS	3.5	1
WAp	1.5	1.25
WCh	3.2	2.4
WPe	2	2.4
W (summary)	2.1	1.9
XSC	3.96	
XSP	1.95	
YCt	4.3 to 5.2	0.7 (?)

involved. (3) The nature of the contact, sharp or diffuse, does not determine the outer boundary of an annual increment. On occasion, a portion of the outer border of an annual increment is diffuse. (4) Different radii give different growth-layer counts. Hence, a whole section is necessary to obtain the true number and true pattern of growth layers at any one level. (5) A "factor of multiplicity" exists for the lower forest border, and must also exist, even though zero, for each tree and every region. (6) Chronological and ecological exactness demand that we make extended measurement and observation in order to obtain the "factor of multiplicity" for any region. (7) Actually, growth layers are the more or less easily visible expressions of growth flushes whose complete record of complex variations is the most highly prized of information but whose activity is difficult to trace.

INTERRELATIONSHIPS

CAUSES

The causes, whether physiologic, ecologic, or specific, underlying the formation of the different types of growth layers and the intensity of the "factor of multiplicity" are of consuming interest because a knowledge of them will permit interpretations. Here will be mentioned only such facts and suggestions as are immediately pertinent to the work.

Climatic.—Those topics which bear upon the climatic causes may be discussed under growth slowdown, frost-induced growth layers, post-seasonal growth, and general rainfall.

Growth slowdown here refers to a transitional stage between continuous cambial activity and its complete cessation within a single growing season. The evidence for such slowdown and notes on weather conditions have been somewhat fully discussed on pages 186-199.

Among the Washington trees there was distinct evidence that low temperature during the rapid growth of spring distinctly retarded elongation. A further bit of evidence may be added. The tree WCh 2 has been described heretofore. Tree WCh 3 grew within 50 feet of WCh 2. Branch WCh 3-2 was measured during the first half of 1945. From April 25 to May 13, scarcely any tip growth occurred. The weather was cool to cold with some heavy frost. During the cold spell the plum trees grew least, the cherries the most, and the peach an intermediate amount.

Interrupted lightwood and interrupted densewood give evidence of growth slowdown which is in contrast with the acceleration in growth processes indicated by divided lightwood and divided densewood.

During the course of fieldwork, it became apparent that low temperature, drought intervals as reflected in low soil moisture, and insect attacks might separately or in combination be responsible for decreased cambial and other growth activities. The cherry tree, WCh 3, gave evidence, as above described, of the repressive effect of abnormally low temperature after growth had started in the spring. In many instances, as in TTP 20, the reason for decreased growth is not directly known.

Growth slowdown, in summary, ranges all the way from an almost undetectable decrease in activity to complete cessation, and the evidence therefore is both external and internal on a branch.

Further influence of low temperature, as well as the effects of low rainfall and of insect attacks, will be discussed later.

Frost-induced growth layers, by the intimate connection of dense-

wood with the frost injury and recovery, give evidence of the cause of such intra-annuals. Other evidences connected with frost, namely, resin canals, compression wood, and parenchyma cells, give almost equally good support to a temperature cause. In some cases the densewood, or other features, alternates tangentially with spots of frost injury and recovery which are scattered around the circuit. In the remainder of the cases, a single unified arc of frost injury is continued around the circuit by densewood, by resin canals, or by parenchyma cells. These features thus either accompany the frost effects or replace them.

Densewood cells, whether isolated, in patches, or in a continuous zone, resemble ordinary densewood. Examples of densewood made by low temperature are numerous. Perhaps the best photographs of them are on plates 1, figure 2; 30, figure 1; 32; and 34. In those instances where frost effects and densewood cells are intermingled, no doubt can arise as to the intra-annual character of the growth layer. However, where the densewood is a continuous band completing the circuit from end to end of an arc of frost injury, the outer margin is commonly sharp, with a sharpness equal to that of an annual increment. The frost injury may disappear longitudinally along the branch and leave an entire band of densewood as part of a *bona fide* growth layer. Frost-induced growth layers, either partial or entire, have been observed in junipers (CMJ 1 and 2, TTJ 2-4), in spruce (TRSp 1 and 2), in apple (TTAp 2-3), in Arizona cypress (TTC 5-5, 34-2; XSC 1-3, 2-1, 2-2, 3-1, 3-2, 6-1, 8-1, 8-2, 8-3, 9-2, 9-3, 9-5, 9-6, 10-1, 10-2, 11-2, 11-3, 13-1, 13-2), in yellow pines (TTP 21-2, 21-5, 21-6, 21-7, 21-9, 21-10, 23-1, 23-3, 24-10, 24-12, 24-14), and in Jeffrey pine (XSJf 1-1). Indeed, CMJ 2-1-b appears to have two 1938 frost injuries, the inner one accompanying and causing a sharply bordered intra-annual. In all trees designated TTC, frost-connected arcs and circles of densewood, either diffuse or sharp, are common features. These features of densewood, combined with the many not frost-connected, suggest strongly that the Arizona cypress is highly sensitive to slight changes in habitat factors, one of which is certainly temperature. The most pertinent evidence of the role of frost in producing growth layers comes in the intimate association of densewood cells with frost-effect pockets where densewood and frost injury alternate around the circuit of a cross section.

Longitudinal transitions and interrelationships illustrate even more clearly that growth layers can be formed by low temperature *within* the regular growing season. Transitions occur either inward or outward on a branch. A continuous circle of frost injury and recovery

on one section changes within several centimeters to an arc of frost injury, or a series of separated arcs, whose circuit is completed by densewood. Farther along the branch, frost effects disappear entirely and leave a continuous band of densewood. Such transitions have been noted particularly in the apple, the Arizona cypress, and the pine. One of the best examples was noted in XSC 9-5 where 9-5-a, 52.5 cm. from the tip, contains a complete circle of frost in 1938, with which densewood cells are associated. In 9-5-b, at 48.5 cm. from the tip, no change has occurred. In 9-5-c, at 42.5 cm. from the tip, the frost effects are much subdued and the band of densewood is complete and entire. In 9-5-d, at 33.5 cm. from the tip, direct frost injury and recovery are absent but are represented by diffuse densewood.

Resin canals, compression wood, and parenchyma cells are associated with, or substituted for, frost injuries in the same manner as the densewood cells. The first two occur rarely but the parenchyma cells are as common, although not as continuous, as densewood. Commonly, an arc of frost injury is completed around the circuit both by densewood and by parenchyma cells. Thus these last, like densewood, appear to indicate an interruption in the normal course of growth not long after the start of growth in the spring. Many annual increments not only have parenchyma cells connected with frost injuries but also have circles of such cells farther out in the xylem (at times associated with densewood) which was formed much later in the season. Perhaps it is reasonable to suppose that these circles of parenchyma cells are also caused by some interruption in the normal course of growth. They have been studied especially in the Arizona cypress, the cottonwood, the Siberian elm, and the juniper. In a longitudinal direction, a circle of parenchyma cells may represent the frost injury existing elsewhere on the branch. Within a space of 20 cm., on XSC 11-1 (pl. 30, fig. 1), a complete circle of frost injury in 1938 becomes very much subdued and is replaced by densewood and parenchyma cells. In branch XSC 11-3, the frost injury is entirely absent leaving only the densewood and the parenchyma cells (pl. 31, fig. 2), all within a distance of 3 cm. The use of parenchyma cells as a dating medium in place of the frost injury they are supposed to represent must be carried out with great care, if at all.

If frost strikes before the cambium becomes active around the entire circuit of a branch, an interior lens may be formed. Frost-formed interior lenses are fairly common and have been observed chiefly in Arizona cypress (for instance, XSC 1-2, 1-5, 4-1, 13-3) and in pine (TTP 21-3, 24-10, 24-14, XSP 2-2, 2-3). In XSC 1-2, a frost injury is directly associated with the densewood of the lens. In XSC 1-5, the

frost injury of the interior lens stops short of the full length of the lens. The injury is continued by a fairly sharp densewood band. The length of the lens depends, of course, upon the amount of cambium which was active and which had set off xylem cells at the time of impact of low temperature. TTP 21-3 is an interesting case. In sections *a*, 26 cm. from the tip, a sharply bordered interior lens containing frost injury and recovery extends for 90° around the circuit. In sections *b*, 5.5 cm. from the tip, an arc of densewood represents the lens and injury of *a*. The increment for 1941 in TTP 24-10-a contains a concurrent interior lens system, each member of which contains a frost injury so intimately connected with the densewood that no doubt can arise as to the cause of the lenses. The 1941 increment of TTP 24-14-a possesses an interior lens caused, very probably, by low temperature (pl. 19, fig. 2). Frost-injured cells are accompanied by irregularly shaped cells with thick, heavily lignified walls and both narrow and wide lumens. Under anything except high magnification of stained sections, the interior lens appears to be an integral part of the densewood of the previous growth layer.

The substance of the work on temperature shock shows rather clearly that the effects are twofold: (1) anatomical, chiefly in the production of frost injury and recovery, with the accompanying parenchyma cells, resin canals, and compression wood, features commonly, but not universally, restricted to the branches; and (2) physiological, chiefly in the formation of densewood and the deposition of gums, resins, and tannin, effects probably not restricted to any one part of the tree body above ground.

Postseasonal growth may properly be applied to any growth occurring after the grand and unified period of growth which follows winter dormancy. It may be present as a complete, entire growth layer, as a lens or series of concurrent lenses complete or incomplete, as isolated cells, or merely as an extension of the terminal bud. In any case, postseasonal growth indicates that the cambium has been stimulated to activity at least a second time within the same general growing season or during the following autumn or winter.

On November 16, 1939, nine trees were moved from the Experiment Substation to the Conservatory where light, water, and heat were supplied. Growth, which had ceased previously for the 1939 season, was reinitiated, and the resultant "Conservatory growth layer" was either lenticular or entire. Some of the sections were cut from branches while growth was in progress. The response to warmth and moisture simulating summer conditions, even in the presence of shorter day-lengths, was decided. It indicates, along with the wealth

of other evidence, that the formation of xylem and the nature of the growth layers depend upon the variations of growth factors not only during the so-called growing season but also throughout the year. In some cases, the Conservatory growth layer is separated from the chief 1939 growth layer by a transition zone which makes identification and dating simple; in other cases, the separation is much more definite. Hence the nature of the growth layer, whether annual or intra-annual, depends upon the variations in the impact of growth factors, variations which may or may not be annual, and which may or may not be sufficiently intense to make either annual or intra-annual growth layers indistinguishable, one from the other.

Tree TTP 20 had more constant observation over a longer interval of time than any of the other trees. Late in the autumn of 1939 the terminal buds expanded and elongated. The following is quoted from notes written December 14, 1939, when sections were taken: "A branch from the south-southwest side. Buds full and much elongated. Taken after a warm autumn, with rain several weeks ago. (Has a lens been made?)" The increment for 1939 in TTP 20-2-a, 44.5 cm. from the tip, possesses a long exterior lens that appears sharp under low-low power but indefinite under low. In TTP 20-2-b, 24. cm. from the tip, the lens of *a* has become an entire growth layer whose inner margin varies from sharp to diffuse under low-low power. The outer walls of the outer cells of the added growth layer are incomplete and the outer margin irregular. In TTP 20-2-c, 12 cm. from the tip, the densewood underlying the "extra" growth layer of 1939 has become so diffuse and weak that, although it has the position of the lens and "extra" growth layer of the previous sections under low-low, under high power it loses its identity as densewood. The outer walls of the outermost cells of 1939, and in many cases the complete cells, are immature, and the outer margin of the increment is highly irregular. In TTP 20-2-d, 2.5 cm. from the tip, resin canals around the circuit seem to occupy the radial position of the intra-annual densewood which exists farther inward on the branch. The outermost margin in *d* has, in places, typical densewood cells rather than the partially immature cells and irregular margin farther inward.

Postseasonal growth appears to indicate a persistence or return of conditions which stimulate growth after the grand growth period has been completed earlier in the season. The presence of postseasonal growth depends, apparently, not upon the time of cutting of sections so much as upon the presence of growth-stimulating conditions.

The following branches are examples of postseasonal growth for the year 1940.

TTC 5-2 (cut March 25, 1940)

Sections *a*, 87 cm. from the tip: 180° lenses one cell thick represent 1940.

Sections *b*, 67 cm. from the tip, show the same growth.

TTC 5-3 (cut June 23, 1940)

Sections *a*, 91 cm. from the tip: 1 sce and 1 s lens plus 1 d lens for 1940.

TTC 5-4 (cut July 17, 1940)

Sections *a*, 87 cm. from the tip: 1 wide sce for 1940.

Sections *b*, 47 cm. from the tip: 1 narrow ce for 1940. Here the sharpness of the outer margin subsides outward on the branch.

TTC 5-5 (cut August 1, 1940)

Sections *a*, 56 cm. from the tip: 1 sce plus 2 s lenses for 1940.

Sections *b*, 16 cm. from the tip: 1 sce only.

TTC 5-6 (cut August 17, 1940)

Sections *a*, 89 cm. from the tip: 1 sce plus 1 psL plus a 100° incomplete lens, one to two cells thick, for 1940. Here the immature growth may well be post-seasonal.

Sections *b*, 45 cm. from the tip: 1 sce plus 1 msce plus 1 ms lens plus a series of short, unligified, incomplete lenses of postseasonal growth for 1940.

More growth occurred in *b* than in *a*.

TTC 5-7 (cut September 10, 1940)

Sections *a*, 74 cm. from the tip: the annual increment for 1940 contains 1 sce plus a slight hint of postseasonal growth of a cell or two just under the cambium.

Sections *b*, 41 cm. from the tip: have, in contrast, 1 sce plus 1 d lens plus postseasonal growth of two immature, incomplete lenses one cell thick.

TTC 5-8 (cut September 28, 1940)

Sections *a*, 72 cm. from the tip: 1 sce plus 2 s lenses plus psg for 1940. The psg consists of scattered cells and two short lenses, all of immature cells.

Sections *b*, 14 cm. from the tip: 1 sce plus 1 s lens plus psg. Only an immature cell or two represents the psg this far out on the branch which has increasing multiplicity inward.

TTC 5-9 (cut November 9, 1940)

Sections *a*, 69 cm. from the tip: one long concurrent s lens system plus a few immature cells as postseasonal growth for 1940.

Sections *b*, 34 cm. from the tip: no postseasonal growth could be seen.

TTC 5-10 (cut February 1, 1941)

Sections *a*, 53 cm. from the tip: no visible postseasonal growth.

Sections *b*, at 36 cm., show the same.

What postseasonal growth may look like, in some cases, after another season has passed is probably illustrated by TTC 34-4-a, cut off November 29, 1941. The entire outer contact of 1937 is irregular and ragged. Collapsed green cells are followed by one or two rows, in most cases, of rather narrow, heavily lignified, thick-walled cells, under the succeeding typical lightwood. It seems probable that some growth was taking place after the regular growth of 1937 had been finished and before low temperature affected the cambium. This type of end to a season is not at all rare. In TTC 34-4-c, 12 cm. outward from *a* and 50 cm. from the tip, the densewood of 1937 is separated into two bands by one to two rows of wider cells which are immature and crushed. Under low-low power this appears to be an extra growth layer.

The end of January and the first part of February 1942 experienced two weeks of exceptionally warm weather with effective rains, followed by several days of freezing weather. Because of the high temperatures seven branches were sectioned February 21, 1942, to ascertain whether or not the cambium had been stimulated into activity. TTC 33-8, sectioned 33 and 17 cm. from the tip, was definitely not growing in the sense that new cells were being set off. However, the cambium is two to three cells in thickness and full of cytoplasm; in sections *b* especially, the cambial initials are prominently nucleated.

Sections TTL 3-5-a were taken 5.5 cm. from the tip. The outer margins of the xylem are wavy and irregular in part. The cambium, six cells thick, seems to have been active at the time of cutting; the swollen cells are full of cytoplasm and prominently nucleated.

In TTM 1-5-a, taken 14 cm. from the tip, the above situation is repeated.

In TTP 20-17-a, 13.7 cm. from the tip, the outer margin of 1941, irregular on the whole, contains many immature cell walls. The cambium, three to four cells thick, was in excellent condition, its large cells full of cytoplasm. At 2.5 cm. from the tip, in TTP 20-17-c, the situation is the same.

The cambium in TTCw 1-4-a, 10.5 cm. from the tip, appears to have become active just before cutting. The band of cambial initials is three to four cells thick, each cell rich in cytoplasmic contents.

On TTP 24-9 the terminal bud had just expanded and lengthened. TTP 24-9-a, 8 cm. from the tip, shows no growth added to 1941. Cambial cells are narrow, and conspicuously nucleated only locally. In TTP 24-9-b, 1.5 cm. from the tip, over an arc of about 45°, translucent, immature cells of moderate size had been added to the mature xylem of 1941. Here the cambium was in better condition than in *a*.

But the striking feature in both *a* and *b* is the condition of the rays where they pass through the cambial region. The individual cells are very much enlarged, full of cytoplasm and conspicuously nucleated.

In TTE 2-4-a, taken 13 cm. from the tip, the mature xylem of 1941 is surrounded by a broad cambial zone which consists of cambium plus immature tracheids and vessels just set off. Here there was definite growth during midwinter.

C. D. McGeehee, Superintendent of Lubbock City Parks, reported in February 1942 that the pines, junipers, and other gymnosperms of the Nineteenth Street Park had grown a tip flush during December 1941. On the pines this amounted to more than a half inch. Our own observations confirm the report.

It seems clear, therefore, that cambial activity can be stimulated and growth initiated at any time of year, even during midwinter, if conditions become propitious. In regard to the particular period of a certain intensity of growth-stimulating conditions during the winter of 1941-1942, a definitely specific response occurred; the Arizona cypress, the honeylocust, and the maple responded least while the pine and the elm responded most.

One point, having to do with postseasonal growth and temperature effects, remains. It is of major importance because it appears to link the closing phases of regular-season growth and postseasonal growth during the winter. In TTC 30-2-a, 67 cm. from the tip, the outer densewood of the 1937 increment shows the following sequence: (a) A densewood zone sharp on its outer margin, (b) two rows of light-wood cells crushed as if by frost, and (c) two to three rows of densewood whose outer contact is slightly ruffled by offsets in alternate radial columns. The increment for 1938 in its outer portion shows the following: (a) The start of densewood, (b) a narrow zone of flattened, unlignified cells, and (c) the remainder of the ordinary densewood. Because of the sequences, as given in both 1937 and 1938, the outer margins become increasingly indefinite when viewed under decreasing magnification. The zones of immature and crushed cells in both increments have the appearance of the effects of an autumn frost which was preceded and succeeded by postseasonal growth. In sections *b*, 46.5 cm. from the tip, the sequence of 1938 in *a* is repeated. Sections of TTC 34-1-a, *b*, and *c* differ from the above in lacking the outermost densewood cells; instead, the outer cells comprise the immature zone of crushed and cupped cells with cells added here and there after the crushing. Either the outermost cells of 1938 densewood zone were left immature or else postseasonal growth was added

late in the season just before frost crushed it. Low magnifications give such contacts a very indefinite appearance.

The linkage and relations between the closing phases of regular-season growth and postseasonal growth, where present, determine in large measure the definition of the outer margin of the annual increment. There is, of course, the ideal margin whose appearance in cross section is a smooth curve abruptly separating the narrow, thick-walled, heavily lignified cells of densewood on one side from the large, thin-walled, slightly lignified cells of lightwood on the other. The definite cessation of growth was followed some time later by a decisive, prolonged, and even an explosive burst of cambial division and cell enlargement. This is the ideal concept of a growth layer, or commonly called "annual ring," and of a boundary between two of them. Unfortunately, all growth layers are not so well formed nor all contacts so sharply defined. Where conditions fluctuate decisively for prolonged intervals between those promoting and those prohibiting growth, the appearance and the margins of the growth layers approach the ideal, but where the conditions fluctuate less decisively over rather short intervals on both sides of the conditions separating growth from nongrowth, the appearance of growth layers recedes from the ideal concept and the margins become blurred for any one of several reasons. Such indefinite contacts are due either to irregularity of margin or to added growth, both of which are common features in the branches of the trees under study at the extreme lower forest border.

Investigation of the outer margin of the xylem just under the cambium has yielded a mass of information which can be used for an understanding of the contacts between two growth layers in xylem away from the cambium. Briefly, the outer margins of densewood are irregular because (1) alternate radial columns of xylem protrude into the cambium which loops over the columns, (2) alternate groups of columns protrude, (3) outer cells in alternate columns or groups of columns enlarge rather than remain narrow as in typical densewood, (4) outer walls of the outer cells remain thin and nonlignified singly, in groups, or collectively. To what extent these features are postseasonal is problematical. Undoubted additional, or postseasonal growth takes several forms: (1) Isolated large cells here and there under the cambium; (2) isolated groups of cells in the form of incomplete, immature lenses; (3) a zone of postseasonal growth entire over the circuit; or (4) a typical compact zone of densewood grading outward into cells increasingly larger, thinner walled, and less lignified. Every exterior lens and "outer thin" growth layer is postseasonal growth in a very definite sense. It should be added that the four types of irreg-

ular margins and the first three forms of postseasonal growth apparently are somewhat more typical of interseasonal growth rather than of intraseasonal.

The intensity, and perhaps the duration, of the impact of alternating growth-promoting or growth-prohibiting factors determine when and how often trees put down xylem. Insofar as visible results are concerned, certain environments probably have one grand and no secondary growth periods a year whereas others have multiple periods in a year. Such secondary periods are well known; the resultant additional growth ranges from an expanded bud or a single tracheid to an extra tip flush or a sharp, complete, entire growth layer so clean-cut it would be "counted" as an "annual ring." Of course, the sharp, complete, entire intra-annuals are not too common even at the lower forest border. These added to the sharp lenses create an error as high as 15 percent or more in a straight count of "annual rings" in trees grown under lower forest-border conditions. This is the factor of multiplicity.

The influence of rainfall, or more properly speaking, the control exerted by fluctuations in soil moisture, is of prime importance to tree-growth studies, and an extensive study of it goes far beyond the scope of the present work. Water, of course, has a critical place in physiological processes; it is fundamental to the hydrostatic system of trees. Some students emphasize the role of water. But if water is a controlling factor in certain habitats, one must weigh carefully the fact that decided alternations of wet and dry periods will alternately promote and inhibit growth, no matter in what part of the general growing season they occur. Other students stress the combined influence of many growth factors. Unless an attempt be made to isolate one factor in order to determine its influence on tree growth, much information, both on tree growth and on climate, may remain unknown.

At the present moment, only such notes on the influence of rainfall will be given as are connected intimately with this study. The apple tree, WAp 1, was closely observed throughout 1944. Tip growth had practically ceased by June 11, and a covered terminal bud was set by June 14. This was also true for WCh 3. For the last week of May and the first two of June, the temperatures were high and rainfall was ineffective. Until April 29, the spring had been humid and cold, growth had been severely retarded. Scattered showers of little or no effectiveness marked June and July with the exception of a severe storm and heavy rainfall of June 19, an inch or more of rain falling the night of July 13-14, and a heavy rain the night of July 19-20. Temperatures were high. In any case, a portion of the branches on

trees WAp 1 and WCh 2 began a second tip flush during the week prior to July 23. About five days prior to the initiation of tip growth, the moderate crop of apples had been removed from WAp 1. The growth on WCh 2 indicates that this removal was not the inciting factor. The second tip flush on WAp 1 varied from 1 to 4 cm. in length and had been completed between the 6th and 13th of August. At the end of a period of high temperature, a rain of 6.2 inches fell on August 2. The temperature remained low until August 11 when it rose sharply to remain high until August 18. Between the 13th and the 20th, a few of the covered terminal buds on WAp 1 expanded and burst open. Growth impulses had not yet ceased because on October 22, a 4-foot plum tree within 60 feet of WAp bore scattered blossoms chiefly on branches from which the leaves had dropped. Late in November a newspaper carried a notice of the presence of cherry blossoms at the Tidal Basin in Washington.

The main points of WAp 1 and WCh 2 history are paralleled by WPe 1 except that in WPe 1 the second flush began immediately after July 23 rather than just prior to that date, and except that growth continued until August 27. On the peach tree, the tips commonly withered and died. One-third of the branches on WPe 1 grew second flushes.

Qualitative, with a slight admixture of quantitative, work is highly suggestive as regards the effects of growth factors, but controlled experimental plots of trees would no doubt give us much more precise information. Nonetheless, the observations of 1943 are perhaps worthy of record. Trees and shrubs observed were apple, peach, red cherry, black cherry, plum, oak, chestnut, dogwood, gooseberry, and currant. Second flushes were present and common on all except the one small cherry which was the last to leaf out in the spring.

Weather notes were taken as follows: Winter 1942-1943, dry; spring 1943, normal rainfall; last three weeks of June, no rain, hot with temperatures over 90° F.; first two and a half weeks of July, normal with periodic, but not too effective, rain; rest of July, rainless; August 17, "0.17 inches rain last night, first effective rain since June 5"; up to August 23, high temperature and no rain; at the end of August and the first of September, several good growing rains. In the midst of the June dry period, the Japanese beetle attacked all trees except the oaks. The attack tapered off the first part of July. Ten to 15 percent of the leaves were attacked except for one plum on which 90 percent of the leaves were affected. Each affected leaf was left 10 to 100 percent dead and brown by the beetles. They left only the veins in the affected parts. With the exception of the plum tree which

was 90 percent affected, the relatively small amount of beetle damage did not seem adequate to cause a second flush. Furthermore, the same branches were not affected, and the damaged leaves were not replaced by new photosynthetic surfaces.

The record of second tip flushes and leaf drop was sketched during the summer. By July 26, the length of the second flush on the various trees varied from 2 to 15 cm. on first flushes of 5 to 30 cm. or more. Two plum trees growing side by side showed, in the one case, distinct terminal bud scale scars between the two flushes of 1943, whereas in the second case, no terminal bud scale scars existed between the two tip flushes. Growth continued at least until July 31. The second flush on the branches of a 12-foot-high oak varied from 13 to 15 cm. to which no further growth was added during the following nine days. By August 8 native, as well as planted, trees had begun to shed their leaves. A large mulberry, near the fruit trees, and gooseberry bushes were losing their leaves. Currant bushes had lost from 50 to 100 percent of their leaves. The second flush on a black cherry tree had grown 15 to 20 cm. beyond the midseason terminal bud scale scars. Several shoots on a gooseberry bush had grown a second flush of 9 cm. whereas the remainder of the shoots on the bush appeared not to have grown any during the season. In the 10 days subsequent to August 8, leaves continued to drop. Now the leaves on dogwood and oak were also dying. Some of the gooseberry and currant bushes had lost all their leaves. They were falling from native large-leaved trees in the woods. Spots of grass in lawns began to die, but this occurred definitely after trees had begun to lose their leaves.

It seems quite clear, not only from the present work but also from that of other students, that the cambial activity wave is complex in nature, has a variable amplitude, and may have a length far shorter than a year. The abundance of intra-annual lenses and the less common intra-annual, sharp, complete, entire growth layers testify to secondary activity waves in the cambium, whereas minor growth layers such as arcs, interrupted lightwood or densewood, and divided densewood or lightwood indicate minor fluctuations superimposed on the larger waves. One wishes that there were always one sharply delineated major wave a year with superimposed waves always revealing themselves somewhere within the crown or trunk of the tree. Without complete dissection of the tree, some of the revealing spots will be undetected, and the magnitude of the factor of multiplicity will be unknown.

Another matter impinges directly upon waves of cambial activity. One or two students have held that drought can so reduce cambial ac-

tivity in time and throughout the body of a tree that the resultant xylem representing an entire year's growth covers but a fraction of 1 percent of the body of a tree (Schulman and Baldwin, 1939). This means, it would appear, that a major portion of the cambium neither died nor set off xylem cells from mid- or late-season of one year until the opening of growth the second year hence; and in case of a compound lens, the third year hence. Several examples could be cited to help explain, at least in part, the problem of a long quiescent cambium, but one will suffice. The increment for 1939 in TTP 24-3-a consists of a series of concurrent lenses when viewed under low power. However, high power shows that the densewood is continuous around the circuit—lightwood is lenticular, densewood entire. The cambium did not fail to divide. At one small locality, the 1940 increment is reduced to two or three rows of densewood cells. Hence, the densewoods of 1938, 1939, and 1940 are in contact and would be interpreted under low power as an absence of 1939 and 1940 increments. Adjacent to the locality of merged densewood, the band becomes divided densewood as lightwood cells are inserted between the respective densewoods.

Nonclimatic causes.—Multiplicity allies itself so naturally with variable factors such as soil moisture, temperature, or defoliation, that it is rather difficult at times to think of genetic causes, the influence of growth hormones, or microhabitat factors. Basically, the influence of heredity and of hormones may be governed by present or past environmental conditions. All are somewhat outside the scope of the present work.

Any genetic influence which causes multiplicity of growth layers, must, it seems, have arisen at a time when the organism did fit the environment and its growth habits were in some way fixed in the genes. Ultimately, according to modern concepts, terrestrial and cosmic environment control life and life processes, from the phylum to the species and from the general to the detailed. What we call genetic may, perhaps in some way, be the transmitted control of past environmental influences. The situation of the current season is complicated and the causal factors placed back in time by the formation of a structure in last season's terminal bud which will grow into two tip flushes the following season. Multiplicity of tip growth inherited from terminal buds needs much more study.¹⁰ As yet, there is no

¹⁰ According to Hustich (1948, p. 32), Hesselman in 1904 pointed out "that the winter bud consists of the same number of 'short shoots' as that which appears on the 'long shoots' the following summer."

known evidence of diameter flushes being predetermined as is possibly the case with tip flushes. Then, too, there are cases of two diameter flushes to one tip flush, and one diameter flush to two tip flushes.

The problem of growth-hormone effects resembles that of genetic effects in that the hormones shift emphasis away from the more obvious and immediate physiologic factors, as controlled by environment, to those factors less obvious and more remote. If hormones alternately promote and inhibit growth, we must search out factors controlling hormone growth rather than factors directly controlling cambial activity, differentiation, and maturation. Those ecologic factors which students have been investigating may apply to either case.

Multiplicity, or the tendency toward, can be induced apparently by factors local to a single tree; for instance, excessive drainage toward or away from the tree, competition, temperature pocket, or soil conditions. In the case of the trees TTA_p 1 and TTA_p 2, the second was irrigated July 25, 1939, and added a second growth layer as well as a second tip flush, whereas TTA_p 1, not irrigated, did not add extra flushes. MacDougal (1936) had performed the same type of experiment at Carmel, Calif., with like results.

Trees from the Texas Agricultural Experiment Substation yielded extreme multiplicity because of periodic irrigation. For instance, XSC 1-3-a, 70 cm. from tip of branch, contained 15 sharply bordered growth layers for four years. Although the multiplicity may be an exaggeration, it is just this exaggeration which teaches what a tree can and will do under certain habitat conditions. Branches, of course, could have effects exaggerated in contrast with the trunk, but available evidence does not support such a view.

A more simple nonclimatic cause of growth variation is suggested by a pear tree, 4 feet high, which grew within a few feet of the Washington series of trees. It had grown a second set of blossoms by May 13, 1945, the first set having been frozen subsequent to April 25. A year prior to this, May 13, 1944, the pear tree was carrying six pears and had tip growth of 1 cm. On the same date in 1945, it had no pears but had tip growth of 45 cm. The production of fruit, identical with a heavy seed year in other trees, may well retard growth.

MULTIPLICITY AND CHRONOLOGY

The effect of multiplicity upon all problems having to do with chronology is a serious matter indeed. It seems clear from the evidence available that multiplicity exists in the lower forest-border region and also that the "factor of multiplicity" varies with the habitat.

Some of the facets on the subject of multiplicity as related to chronology are here outlined.

Anatomical problems.—In the final analysis, certain intra-annuals cannot be distinguished from annuals. Many of the intra-annuals, within the limits of visible area, possess a border which is diffuse anywhere from a small arc to an entire circuit. Such localization of diffuseness exists also in the longitudinal direction. Other intra-annuals, within the limits of visible area, possess a border which is entirely sharp and hence exactly resembles that of an annual growth layer. It may be that somewhere within the body of a tree, no matter how small the area may be, the margin of *every* intra-annual breaks down into diffuseness. If this should turn out to be true, many cases would be beyond our reach because of the impossibility of dissecting completely the entire body of each tree under study.

Annual contacts, furthermore, are not always sharp. In any one out of the following 11 ways, the densewood of the annual may have subsided from a definition of utmost sharpness.

(1) Localized areas of cells on the outermost part of a growth layer, or more or less alternate columns or groups of columns in the densewood region, resemble lightwood cells.

(2) The outer margin of the growth layer has been made irregular because alternate columns of tracheids protrude into the zone of the next outer growth layer.

(3) Scattered parenchyma cells may not only make a margin irregular but also impair definition.

(4) Postseasonal growth commonly causes an irregular, indefinite margin.

(5) Immaturity of outer cells of densewood produces a diffuseness which is striking under low magnification and difficult or impossible to resolve on unstained sections.

(6) Typical densewood fails to form. In TTC 35-7, for instance, sections *a* taken 23.4 cm. from tip of branch, show 3 sec for 1944; sections *b*, at 17.2 cm. from tip, show 3 rather indefinite ce growth layers; and sections *c*, at 12.2 cm. from tip, show 3 diffuse ce growth layers. In sections *c*, no normal densewood cells were present—larger, thinner-walled cells simply follow thicker-walled cells radially with little change in cell size. TTE 1-10-a, taken 60 cm. from the tip, gave an interesting situation in that the 1940 increment is dominated by vessels and has no definite densewood of small polygonal tracheids, whereas the 1941 increment is dominated by tracheids and does have a densewood of tiny irregular tracheids. If the growth layers had not been dated, the 1940 and 1941 increments together would no doubt

have been interpreted as one growth layer. The maples, TTM 2 and 3, possess densewood zones so indefinite or so intermittent around the circuit of cross sections that one would hesitate to call the growth layers annual increments were it not for the fact that the branches had been measured periodically.

(7) Growth is gradually resumed after densewood has formed. This commonly occurs only over a part of the circuit. For instance, six annual increments in TTC 5-7 have short arcs of indefiniteness except in sections *b* where 1938 is indefinite for more than one-half its circuit. The contact for 1938 is diffuse over those arcs radially opposite to the sharp portions of adjacent annual increments. This habit of sharpness opposite diffuseness characterizes intra-annual, as well as annual, growth layers—it is widespread throughout all materials studied.

(8) The outer part of the densewood is complicated by immature crushed or cupped cells mingled with, or followed by, fairly typical densewood cells—as if an autumn freeze had caught postseasonal growth during formation.

(9) The densewood of an annual increment may be a heavy band many cells thick on one radius and a thin stringer one cell thick on the opposite. The Arizona cypress has given many examples of such. In fact, such variation characterizes not only the densewood but also the lightwood. The complete growth layer may consist of one row of lightwood cells and one of densewood cells; or, as described heretofore, it may consist merely of one row of densewood cells. In XSC 6-3-a, cut February 22, 1941, 55 cm. from tip of branch, the following sequence was charted: 1938, multiple densewood; 1939, one to two rows of lightwood cells and one of densewood. This causes an indefiniteness and uncertainty which would make dating impossible were it not for the 1938 frost injury and the known cutting date. As a feature defining the radial margin of a growth layer, a thin “stringer” of densewood is particularly unconvincing as the outer border of an *annual* increment. This is especially true when the growth layer is viewed under low magnification. Thin “weak” densewood is restricted neither to annuals nor to intra-annuals. If it were not for the methods of absolute dating, most of our specimens would have to be discarded.

(10) A sharply bordered densewood band may be followed outward by lightwood cells which are atypical in size and wall thickness. Illustrations exist among Arizona cypresses and ponderosa pines of Lubbock and New Mexico.

(11) The outermost two to four rows of cells in the annual densewood band lack typical densewood characteristics. They may be narrow but at the same time thin-walled and slightly lignified in contrast to the densewood cells immediately to the interior. As a matter of fact, the entire growth layer may be atypical in contrast to neighboring growth layers, as illustrated by 1939-1941 of TTP 23-4-c (pl. 17, fig. 2). If these growth layers are annuals, it is obvious that methods of absolute dating are necessary for their identity. Thus it is clear that the outer borders of annual increments are not all of the same degree of sharpness; they may be less sharp and less well defined than the border of an intra-annual within the same annual increment. An intra-annual, furthermore, may have all gradations from the obviously intra-annual, or "double," to one indistinguishable from an annual.

An "outer thin" growth layer is an expression which has been used in reference to a growth layer extremely thin in contrast to the relatively thick growth layer which lies to the inside and constitutes the bulk of the annual increment. The densewood¹¹ of the outer thin is commonly weaker than the densewood of the growth layer to the inside, although where the inner densewood becomes weaker, the outer becomes stronger on the same radius, and vice versa. The outer densewood may even become indefinite. Absolute dating proves that the outer thin growth layer is intra-annual; in fact, not one case has been proved to be annual. Among the trees used, examples have been found in TTA_p, TTC, XSC, TTJ, TTP, and XSP, chiefly in the years 1939 and 1940. This is a typical notation from an analysis of TTP 20-25-a: "Densewood of inner growth layer is heavy and well-developed, thus contrasting with the densewood of the outer growth layer which is thin, weak, and poorly developed; hence the densewood of the intra-annual is typical of what is expected in an annual, whereas the densewood of the actual annual is weak and atypical in the expected sense." Examples of the outer thin are shown in plates 4, figure 1; 14, figures

¹¹ Douglass (1928, p. 32) referring only to densewood says: "In the process of counting and dating rings in Arizona pines, two sharp red [i.e., densewood] rings sometimes occur close together, giving the appearance of a double and leaving one in doubt as to whether one year or two is involved. . . . If the two red rings [densewood] are unequal in size and the smaller one is inside, that is, nearer the center, it is likely to be a real double formed by the spring drought. If the smaller one is outside the larger, it is probably a separate year. If the two rings are equal and either one shows a further doubling, the two rings in question are separate years." According to this, a "large" (thick) densewood must terminate an annual increment; a "small" (thin) densewood may or may not terminate an annual increment. Absolute dating would appear to weaken the accuracy of the above statements.

1 and 2; 15, figure 1; 25; 28, figure 2; 29; 30, figures 1 and 2; 31, figures 1 and 2; 33; 34; 35, figure 1.

Distinctive configurations in a short sequence of growth layers have been called "signatures" (Douglass, 1934, p. 3; 1937, p. 13) or "fingerprints" (Douglass, 1931, p. 309; 1936, p. 10) and as such are considered a means of identification. One such signature on display

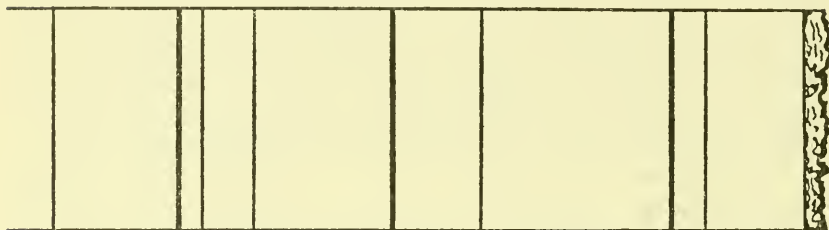


FIG. 45.—Diagrammatic radial sequence adapted from the "signature" used as a cover emblem of the Tree-Ring Bulletin. Each growth layer here shown has been assigned an annual date. Compare with figure 46.

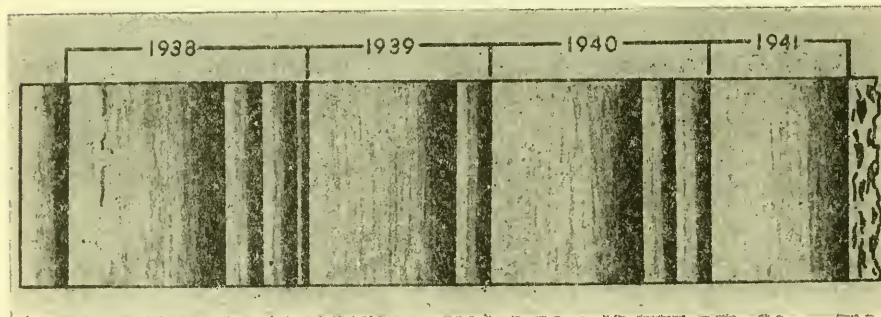


FIG. 46.—"Fingerprint" or "signature" embodied in the growth layers of XSC 12-1-a. Proved dating shows each growth layer not necessarily an annual. Compare with figure 45.

is the one reproduced in part in text figure 45, which served as an emblem of the Tree-Ring Bulletin. The emblem, taken from "Early Pueblo Dating," has been dated (Douglass, 1940, folded plate) as A.D. 422 to 432. Figure 45 should be compared with text figure 46, a specimen dated with absolute accuracy. In the work on TTC, TTP, and XSC, characteristic configurations have repeated themselves monotonously. XSC 12-2-a, cut December 6, 1941, gives the following

alternation of thick and thin, sharply bordered growth layers (text fig. 47) :

- | | |
|-----------------------------------|---------------------------|
| 1. 1 average gl with frost injury | = inner 1938 |
| 2. 1 very thin gl | = "outer thin" gl of 1938 |
| 3. 1 average gl | = inner 1939 |
| 4. 1 very thin gl | = "outer thin" gl of 1939 |
| 5. 1 average gl | = inner 1940 |
| 6. 2 very thin gls | = outer 1940 |
| 7. 1 average gl | = 1941 |

XSC 12-1-a, cut October 11, 1941, gives even a better signature (text fig. 46; pl. 32) :

- | | |
|-------------------|-------------------------------|
| 1. 1 average gl | = inner 1938 |
| 2. 2 thin gls | = outer 1938 |
| 3. 1 very thin gl | = outermost 1938 |
| 4. 1 average gl | = inner 1939 |
| 5. 1 thin gl | = outer 1939, an "outer thin" |
| 6. 1 average gl | = inner 1940 |
| 7. 2 thin gls | = outer 1940 |
| 8. 1 average gl | = 1941 |

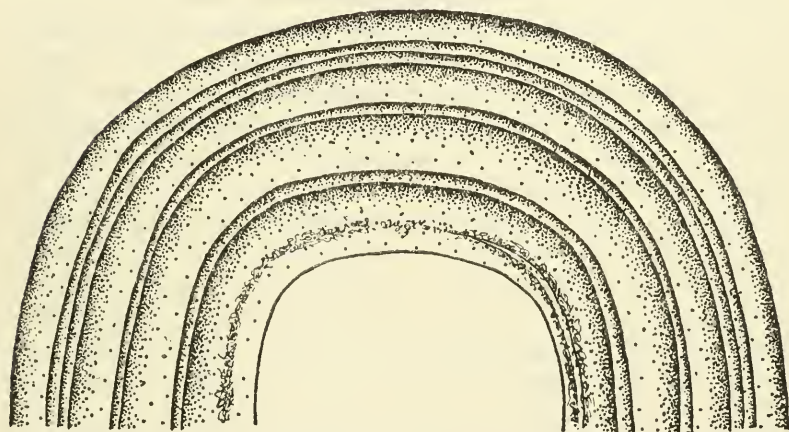


FIG. 47.—XSC 12-2-a. Increments for 1938-1941. Variability of thickness and multiplicity giving a pattern similar to what has been called a "fingerprint." 1 average gl = 1st 1938; 1 very thin gl = 2d 1938; 1 average gl = 1st 1939; 1 very thin gl = 2d 1939; 1 average gl = 1st 1940; 2 very thin gls = outer 1940; 1 average gl = 1941. Without criteria of absolute dating the pattern could be ascribed to growth for 8 years.

All the "outer thin" growth layers have the same general appearance, no matter in which specimens they exist. But it must be borne in mind that trees XSC and TTC were under observation and were dated accurately.

The last phase of anatomical problems has to do with what we have called lenses. Such a growth layer has been called "locally absent" (Douglass, 1939, p. 19), referring specifically to that part of the growth layer which is not there. "Locally absent in places" (Douglass, 1939, p. 19) has been used in the same way. Elsewhere, Douglass (1938, p. 8) has used "often absent," "sometimes absent," and "occasionally absent" in reference to the total absence of the growth layer from the core or cross section in hand. Of course, these may be synonymous with "locally absent" insofar as the remainder of the tree is concerned. In contrast, Glock (1937, pp. 8-10, 48-51) referred to a lens as a "locally present" growth layer. His use of "missing" and "absent" rings refers only to the specimens in hand.

A high percentage of the lenses examined in the present work proved to be lenses only insofar as the lightwood is concerned, the densewood being continuous around the circuit in immediate contact with the densewood of the previous growth layer. The same thing had been noted previously by Douglass (1928, p. 32) and by Glock (1937, p. 73), no doubt under lower magnifications.

In the present work, out of some thousands of examples, all lenses were proved to be intra-annual with the exception of less than half a dozen. The lenses of the exceptions were in all cases the outermost growth layers lying just under the cambium in the position which would be occupied by temporary lenses. No case is known where xylem lay outside the annual lenses. In at least some of the exceptions the densewood was entire around the circuit.

Sampling problems.—The different sequences on different radii of a single section as well as along the longitudinal extent of a branch, so abundantly illustrated heretofore, make it quite clear that sampling problems have a real existence. An increment core is essentially a single radius, and a cross section is a group of radii emerging in the same plane from a single point on the axis of branch or stem. In anatomical work having to do with growth layers such as arcs, half-lenses, lenses, and complete, entire growth layers with variable marginal definition, all grown at the lower forest border, a single radius or even an entire cross section gives an inadequate picture of what the individual growth layers do throughout the tree. A sequence of sharply bordered growth layers on one radius may be duplicated in numbers on a second radius but not by the same growth layers which were sharply bordered on the first. Variability, its nature and amount, has been amply illustrated previously. How misleading one radius can be or how much in error the matching of two radii, growth layer to growth layer, can be, is well shown by a comparison of different radii,

from simple to complex, on TTAp 2-3-b (text fig. 38), TTC 33-6-a (text fig. 5), TTC 12-9-b (text fig. 33), XSC 2-2-c (text fig. 40), and TTC 36-7-b (text fig. 25). Clearly enough, the student should be well aware of the disadvantages of a single radius or of a cross section and should buttress his work by a thorough investigation of the growth habits of the trees with which he works.

Visual problems.—Stained sections under a microscope have many advantages over unstained sections under a hand lens or wide-field binocular, especially for anatomical work. These advantages are well known to botanists.

Although lumens are visible under a hand lens if the surface has been well prepared, such visibility cannot, of course, be compared with that under a compound microscope. The densewood, its resolution and its outward termination, must be seen with all possible clarity. The margin of any given growth layer appears to increase in sharpness as power of magnification used decreases, unless the cells of the light-wood immediately outside the margin are unduly lignified. In this latter case the true sharpness only comes out under high powers. A hand lens has two advantages: (1) it is easy to carry, and (2) in a way, it summarizes anatomical features by omitting details. These details, however, may carry highly important ecologic information.

Extremes of multiplicity.—Previous pages have carried information on the multiplicity typical of the accentuated forest-border environment on the southern High Plains. Certain species and certain years show extreme numbers of intra-annuals whereas others show only a few. In some species, it is impossible to find a year lacking multiple growth layers. The reason for such multiplicity has commonly been held to be large and repeated fluctuations of soil moisture.

The practice called tree-ring analysis, or dendrochronology, has presumed accurate dating to the year centuries in the past by the method of matching thin growth layers in one tree with those in other trees, whether they grew close together or tens of miles distant. If an extremely thin, entire growth layer, or a lens, appears in a certain place on the sequence in one or several trees and does not appear in the other trees of a group, it is designated a "missing" ring and is added to the sequences of the latter trees in order to fill out the supposedly correct number of "years." This undoubtedly is what Douglass (1936, p. 12) meant when he said, "At the very desert edge the trees may become difficult from absence of rings." Perhaps it is not the lack of rings in some of the trees so much as it is their superabundance in other trees that creates difficulty and often leads to incorrect dating. Many trees at the edge of the desert possess so many

partial growth layers and so many very thin growth layers in contrast with certain of their neighboring trees that cross-dating is hopeless.

The chronology and interpretations arising from the matching or cross-dating of growth-layer sequences have been accepted by some because they are based upon so-called "absolute dates" (Antevs, 1948, p. 168) derived from trees which grew "on steep slopes underlain by pervious rocks and near the lower or dry border of the forest." Thus the conclusion cannot be evaded that one of two things must be true: either (1) the minimum number of years represented is equal to the maximum number of sharply bordered growth layers in a group of specimens, or (2) the reader of rings possesses the infallible ability to determine the extent of the annual increment, no matter how multiple it may be or how sharply bordered the intra-annuals.

"Absolute" dates based upon the matching (or cross-dating) of sequences from different trees, in the sense used above, scarcely approach the accuracy of dating in the work reported upon here. In our work, something like 99 percent of extremely thin, entire growth layers and lenses are intra-annual.

The effect upon chronology of counting these thin, entire growth layers and lenses as true annual increments is quite obvious.

Insofar as a calendar year is concerned, every region has its factor of multiplicity. It no doubt approaches a maximum in certain desert and desert-border trees such as mesquite and oak, and in citrus at Yuma, Ariz., which grows after each irrigation. It decreases somewhat at the extreme lower forest border and then continues to decrease toward the forest interior until it probably reaches zero. In and near the lower forest border, the minimum value of the factor of multiplicity closely approximates the total number of extremely thin, entire growth layers plus the number of lenses. The factor, in short, depends upon habitat and species.

MULTIPLICITY AND THE FOREST BORDER

The character of growth-layer sequences, as well as the soil-moisture regime, change from the desert border up into the forest interior. At the extreme lower forest border, sequences are highly variable, that is, they comprise a series of intermingled thick, thin, and partial growth layers. The factor of multiplicity has a high value. Toward the interior of the forest, variability decreases until the sequences become uniform, that is, they include only growth layers closely approaching each other in thickness. At the same time the factor of multiplicity approaches, and may reach, zero. Soil moisture, as condi-

tioned by rainfall, undergoes large and frequent fluctuations from the wilting coefficient to field capacity at the extreme lower forest border. Toward the forest interior these fluctuations subside until, finally, soil moisture remains sufficiently constant to produce uniform sequences and to tend toward unity of the annual increment.

Although the present work has dealt specifically with tree growth of the extreme lower forest border on the High Plains of Texas, sections were also obtained from trees growing under plentiful moisture and short seasons (pl. 3, fig. 2) and from trees growing under very low moisture and long seasons (pl. 36, figs. 1 and 2). Thus the sections at hand illustrate a range of conditions from high elevations in New Mexico to the desert (and irrigation) at Yuma, Ariz.

Those workers (Douglass, 1931, pp. 306-307; 1936, pp. 11-14; 1937, pp. 14-19; Antevs, 1948, pp. 168-169) who use growth layers to date prehistoric events believe that cross-dating, which exists in its most beautiful form in the lower forest-border trees of the Southwest, proves the annual nature of the individual, sharply bordered growth layer and also proves rain to be the controlling growth factor. Growing conditions may be such during a season that the following sequence occurs in some trees: formation of a sharp, complete, entire growth layer; dormancy of cambium; reinitiation of cambial activity; formation of a very thin, entire growth layer or a lens; and cessation of growth. In other trees the second diameter flush does not occur. If the above sequence occurs, it seems reasonable that the thin, entire growth layers or lenses would cross-date among those trees containing them. They would be designated as "missing" from the remainder of the trees. The fact that the thin, entire growth layers or lenses match from one tree to another does not prove their *annual* character.

Uniform sequences of the forest interior do not lend themselves qualitatively to visual cross-dating. Here, rainfall must be close to the optimum amount insofar as visual differences in growth-layer thicknesses are concerned. Where rainfall drops below the optimum periodically, variability of growth-layer sequences increases, and cross-dating becomes possible. The farther and the oftener it drops below the optimum, within limits, the more obvious and the more perfect the cross-dating. But below the optimum is precisely where multiplicity can, and does, occur. Excellent cross-dating and multiplicity, thus, go hand-in-hand, at least in the lower forest border.

The thought stemming from the evidence at hand may be put another way. The more extreme the forest-border conditions are, along with thin soil and steep, rocky slopes (Antevs, 1948, p. 168),

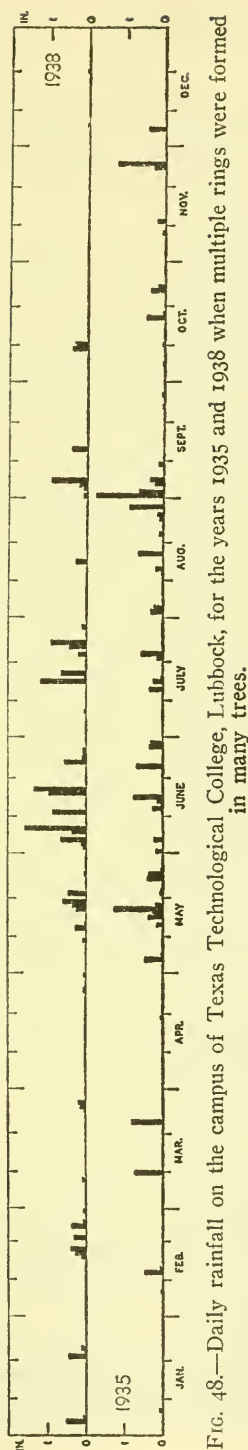


FIG. 48.—Daily rainfall on the campus of Texas Technological College, Lubbock, for the years 1935 and 1938 when multiple rings were formed in many trees.

the greater the separation of individual rains (text fig. 48), the greater the soil-moisture fluctuations, the greater the variability of the growth-layer record, the greater the number of partial growth layers, and the greater the factor of multiplicity. Trees on steep, rocky slopes with little soil depend rather directly upon rainfall, to be sure. However, individual rains, widely spaced in time as they are in the lower forest border, can bring about variations whereby conditions suitable for tree growth, from the standpoint of soil moisture, are terminated and reinitiated one or more times during a general growing season.

If the upper limits of the ponderosa pine zone in the Southwest represent the forest interior with near optimum soil moisture, then we may observe the increase of variability and all it implies downward through the ponderosa pine zone, the piñon, juniper, and oak, to the desert mesquite. Increase of multiplicity does not necessarily accompany increase of variability but, if the work on the southern High Plains is a criterion, the two do increase together in the Southwest. Arizona with its two rainy seasons—winter and summer—would be expected to break into multiplicity very soon with decreasing rainfall, especially because of the intense drought of late spring—early summer, which separates the end of the winter rainy season from the summer rainy season.

The loblolly pine (Con T), introduced to the Lubbock area from a wetter climate, grew multiple growth layers in both trunk and branches even when watered periodically throughout the summer.

All the present investigations emphasize the intimate relationship between excellent cross-dating and amount of multiplicity—both, along with other features, being highly characteristic of the lower forest border in the Southwest.

MULTIPLICITY AND RAINFALL INTERPRETATIONS

It has been seen that sharp boundaries on growth layers do not mean the end of the annual growing season and that multiplicity characterizes the extreme lower forest border. The errors inherent in tree growth-rainfall comparisons are quite obvious if each growth layer, irrespective of its annual or intra-annual character, is compared either with annual rainfall or with the rainfall of some period within the year.

The grave error arising from the use of multiple growth layers as annual increments needs no further comment.

Without doubt, growth-layer thicknesses should be compared with amount of soil moisture, if such data were available, because amount of soil moisture available to plants depends upon factors other than simple rainfall quantities. This is even more true perhaps in the case of intra-annuals. Here a knowledge of the time of occurrence of the widely spaced rains of the extreme lower forest border (text fig. 48), or the fluctuations of soil moisture incident thereto, is of no help unless the exact time of formation of intra-annuals within the general growing season is known. Soil-moisture fluctuations point out the intervals when growth can occur, other factors being favorable, and, conversely, a knowledge of the exact intervals when growth occurs can point out when, other factors being favorable, the amount of soil moisture conducive to growth in a given locality is present. The comparison of intra-annuals with soil-moisture fluctuations within a season is of great significance and awaits close investigation.

Insofar as the transpirational stream is concerned, a tree depends upon the soil moisture immediately present in the ground when growth occurs. Rain that has fallen before growth started and has run off, evaporated, transpired, or percolated out of reach can have no influence on subsequent tree growth; rain that falls after growth has ceased for the year can have no influence on the preceding growth. This sounds elementary, and yet numerous cases exist wherein tree growth has been correlated either with annual or less than annual rainfall, and the student making interpretations therefrom will speak of wet and dry "years." One month or a succession of several months in a year with high rainfall does not mean that other months will have high rainfall or even rainfall above average. Indeed, Henry (1931) says that in the year 1930 in Arkansas, January had 223 percent, May 200 percent, June 22 percent, and July 19 percent of normal; the entire year averaged 96 percent. Much tree growth in a season does not

mean a wet *year* and, where it does correlate closely with seasonal rainfall, such correlation does not necessarily encompass the entire year. It is, however, during the period when growth occurs that a combination of factors closer to the over-all optimum than to the average, creates good growing conditions and therefore much tree growth.

Postseasonal growth, no matter when it occurs, whether soon after the main growing season or during the following winter, poses a difficult problem for the student who correlates tree growth with rainfall at the lower forest border.

MULTIPLICITY AND CYCLE INTERPRETATIONS

Even if cycles were not intriguing, it would be proper and it would be a duty to hunt them out wherever possible because any repeating pattern in an environmental factor can have high significance for the life forms involved. The search for cycles should, nonetheless, be grounded upon reasonable theory, sound principles, and sharp observation. Superfluous as the words may be to some, it still seems necessary to say that a cycle—its reality, its validity, its length, its amplitude, and its continuity—is no better than the data which apparently yield the cycle. This subject of cycles concerns the present work in several ways.

If a plotted graph of growth-layer thicknesses shows cyclic variations, the natural assumption that they are caused by rainfall fluctuations follows. A reasonable question may then be asked: If cycles in growth-layer thicknesses are held to mirror cycles in rainfall, then should not the rainfall itself show the same cycles in simpler, purer form? Also, certain complications intervene between rainfall and its entrance into the ground, between its entrance and its conversion into soil moisture, between soil moisture and the hydrostatic system of the plant, and between the hydrostatic system and the physiologic processes which ultimately result in the production of xylem and phloem.

Unless growth-layer thicknesses are actually influenced by the rainfall of the entire year, they cannot be expected to reveal the cycles in annual rainfall.

Tree growth commonly has been found to compare more or less roughly with the rainfall of a period less than a year in length (Glock, 1941, pp. 687-689). Therefore, cycles in tree growth could only reflect cycles in period rainfall. Is it theoretically possible to have cycles in, say, spring rainfall? A study of this possibility would seem prerequisite to a study of cycles in tree growth.

All the above applies to growth-layer sequences marked by unity of the annual increment. If some of the annual increments in a sequence contain multiple growth layers, then surely comparisons between thicknesses of individual growth layers and either annual or period rainfall chosen at random are wholly invalid.

The same is true when cycle analysis is performed upon sequences containing multiple growth layers. Perhaps the insertion of multiple growth layers in certain annual increments on a sequence may bear upon discontinuities and phase changes said by some to be characteristic of cycles in tree growth.

It is quite clear that the factor of multiplicity has an important place in the study of growth cycles in trees, and only where this factor is zero or where allowance is made for its effect, can we hope for fruitful results in the important subject of cycles.

VII. EXTENSION OF MULTIPLICITY INTO THE TRUNK

The characteristics of growth layers in branches, especially as concern classification and multiplicity, have been described to the extent that present materials permit. The presence of multiplicity has been established by the methods of absolute dating based upon standards of measured exactness. There remains the task of tracing the characteristics found in branches down into the trunk. Although the trunk does not properly come within the scope of this report, mention will be made of the existing evidence.

Evidence at hand indicates that the types of growth layers and the multiplicity so characteristic of branches continue down into the basal trunk. TTC 12 yielded specimens periodically from 1938 until 1950, when it was felled and dissected. In the winter of 1938-1939, sections were taken from branches, and from the trunk several feet down from the growing point of the leader. Multiplicity was identical in branch and trunk. In the summer of 1950, at the time of complete dissection, trunk sections 84 cm. above the ground showed gross multiplicity within the limits of unstained materials. This was especially true of the interval 1936-1937.

The incidence of multiplicity has been illustrated and described previously (Glock, 1951) for 1935 in the trunk of the Arizona cypress, TTC 12; for 1936-1937, in the trunk of a ponderosa pine; for 1938, in an Arizona cypress; and for 1938-1948, in a cedar (Deodar cedar)

trunk. All carry the same general features in the trunk as they do in the branches, insofar as they have been dissected.

The trees transplanted November 16, 1939, from the Texas Agricultural Experiment Substation to the Conservatory were placed there under conditions which reinitiated growth and caused the formation of a so-called Conservatory growth layer. The loblolly pine, Con T 1, as well as all other "Con" trees, was moved to the grounds of a residence on April 24, 1940; it was observed and measured from the time of its receipt, November 16, 1939, until it was dissected January 16, 1943. At the end of 1939, the tip of the leader (known later as Con T 1-5) stood 140 cm. above the ground and growth added thereto by January 1943 totaled 79.3 cm. The analysis of the main stem and all but two of its branches is shown on text figure 49. Tip growth of 1940 (three tip flushes) and 1942 (two tip flushes) was multiple as shown by measurements and by terminal bud scale scars. Diameter growth was equally multiple, even showing two distinct growth layers in the main trunk for 1940 in hand specimens (labeled in capitals on the figure). Hence it is clear that multiplicity makes little or no distinction between branch and trunk.

The following analyses apply to the leader and its chief branches.

Con T 1-5 (leader) (1941-1942)

- a. 2 sce + 1 dce + d gls + d arcs—3 tfs—2 years.
- b. 2 sce + dce's—3 tfs—2 years.
- c. 1 sce + 1 dce—2 tfs—1 year.
- d. 1 sce—1 tf— $\frac{1}{2}$ year.

The inner margin of the growth layer for second 1942 was indefinite back from its own tip flush.

Con T 1-11 (1940-1942)

- a. 4 sce + L's + arcs—4 tfs—3 years.
- b. 3 sce—3 tfs—2 $\frac{1}{2}$ years.
- c. 2 sce—2 tfs—2 years.
- d. 1 sce—1 tf—1 year.
- e. 1 sce—1 tf—1 year.

Here the diameter increment for each tip flush is sharply bordered, regardless of its annual nature. The above analysis for Con T 1-11 is duplicated in Con T 1-12, 1-13, and 1-14.

Con T 1-15 (3d 1940-1942)

a. 2 sce + 1 dce—3 tfs—2½ years.

b. 2 gls—2 tfs—2 years.

c. 1 gl—1 tf—1 year.

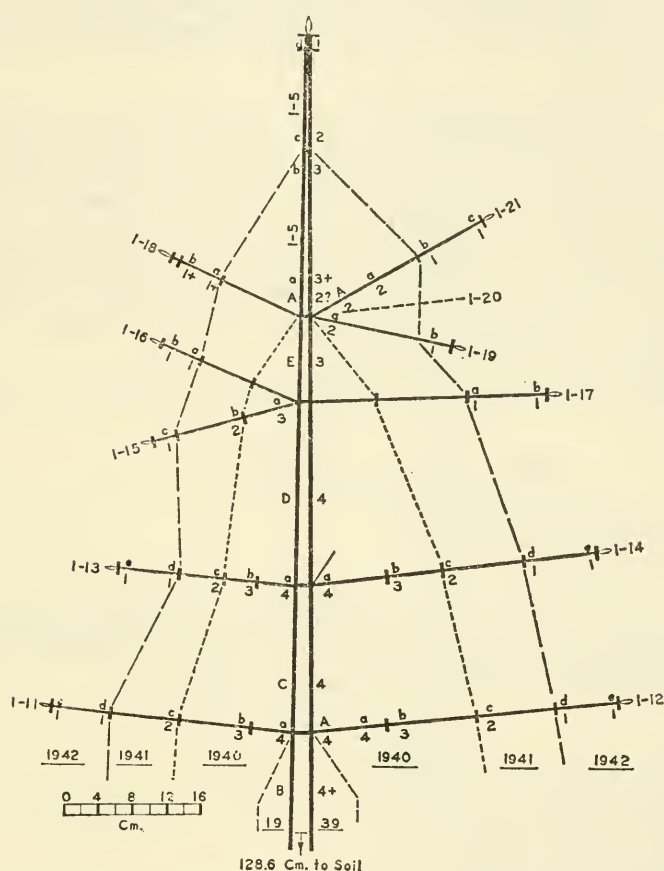


FIG. 49.—Leader of *Pinus taeda* (Con T 1-5) with branches, Con T 1-11 to 1-19 and 1-21, to show annual increase in diameter flushes and tip flushes. Cross-bars represent terminal bud scale scars. Capital letters refer to unstained blocks removed from leader and branches; small letters refer to position of stained sections. Figures opposite letters give the number of growth layers in the sections represented by the letters.

In sections *a* it is to be noted that the contact between 1941 and 1942 is weak and by no means as definite as the border of the intra-annual in Con T 1-14-a.

Con T 1-18 (1942)

- a.* 1 gl + psg—2 tfs—1 year.
- b.* 1 gl + psg—2 tfs—1 year.

Here the second growth flush of 1942 merely added what we called postseasonal growth which served not only to represent the second flush but also served as a factor giving indefiniteness to the main growth layer.

The secondary leader of *Con T 1* (*Con T 1-4*) came off the main stem 11.4 cm. back from the position of the leader tip which stood 140 cm. above the soil level on December 1939. Total tip growth subsequent to 1939 and prior to the time of dissection, January 16, 1943, amounted to 69.3 cm. Analyses, both on hand specimens and under the microscope, are recorded on text figure 50. The tip growth of 1940 on both branch and trunk was multiple. In 1941 both tip and diameter growth were multiple in branch and trunk, whereas in 1942 the same holds only in the trunk.

The following summaries apply to the secondary leader and its chief branches.

Con T 1-4 (secondary leader) (2d 1941-1942)

- a.* 3 sce—3 tfs—1½ years.
- b.* 1 sce + 1 dce—2 tfs—1 year.
- c.* 1 dce—1 tf—½ year.

In sections *b*, farther out the leader than *a*, the margin between first and second 1942 has become indefinite. At *c*, even the outer margin of second 1942 has become less sharp.

Con T 1-6 (1940-1942)

- a.* 4 sce + long arcs—5 tfs—3 years.
- b.* 4 sce + arcs—4 tfs—2½ years.
- c.* 3 sce—3 tfs—2 years.
- d.* 2 sce—2 tfs—1½ years.
- e.* 1 sce + s arcs—1 tf—1 year.
- f.* 1 sce + s arcs—1 tf—1 year.

In 1940, two tip flushes corresponded to one diameter flush, whereas in 1941 two tip flushes corresponded to two diameter flushes, each one indistinguishable from an annual increment.

Con T 1-7 (1941-1942)

- a.* 3 sce + d arcs + psg—3 tfs—2 years.
- b.* 2 sce + d arcs—2 tfs—1½ years.
- c.* 1 sce + 3 to 5 d arcs—1 tf—1 year.
- d.* 1 sce + 3 to 5 d arcs—1 tf—1 year.

This branch contains not only a sharply bordered growth layer for each tip flush but also other growth layers for which there are no visible tip-flush additions. In other words, the activity, or lack of it, in the cambium does not always find its counterpart in the growing tip. Such nonconformity has been well illustrated previously and is further shown in the following branches.

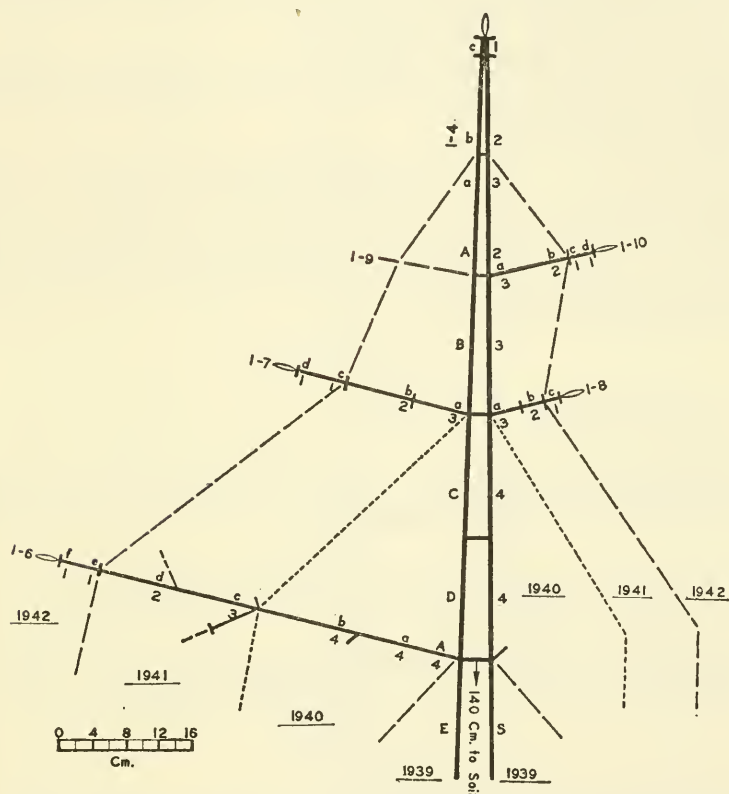


FIG. 50.—Secondary leader of *Pinus taeda* (Con T 1-4) with branches, Con T 1-6 to 1-10, to show annual increase in diameter flushes and tip flushes. Cross-bars represent terminal bud scale scars. Capital letters refer to unstained blocks removed from leader and branches; small letters refer to position of stained sections. Figures opposite letters give the number of growth layers in the sections represented by the letters.

Con T 1-8 (1941-1942)

a. 3 psce—3 tfs—2 years.

b. 2 dce—2 tfs—1½ years.

c. 1 dce—1 tf—1 year.

Con T 1-10 (2d 1941-1942)

- a. 2 sce + 1 psce + dce's + d arcs—2 tfs—1½ years.
- b. 2 sce + dce's + d arcs—2 tfs—1½ years.
- c. 1 sce—1 tf—1 year.
- d. 1 sce—1 tf—1 year.

The psce of sections *a* is no longer present in sections *b* which were taken from the same tip flush. Other branches with a similar reduction in growth layers have two tip flushes.

Both primary and secondary leaders of Con T 1 showed no distinction between branch and trunk insofar as either multiplicity or cambial activity was concerned.

The tree Con T 2 received the same treatment as did Con T 1. The leader tip stood 163 cm. above the soil in December 1939 and added 82.3 cm. growth by May 22, 1944, when the tree was dissected. Here, sections were taken from each of the eight tip flushes which made up the increase in height of the leader from 1940 into 1944. Text figure 51 shows the plan of Con T 2.

Con T 2-14 (1940-1944)

- a. 4 sce + 3 dce + inc—8 tfs—4* years.
- b. 4 sce + 2 dce + inc—8 tfs—4* years.

Although both of these came from the first tip flush of 1940, there is a reduction of one growth layer from *a* to *b*.

Con T 2-15 (2d 1940-1944)

- a. 4 sce + 1 dce + inc—7 tfs—3½* years.

Sections 2-15 came from the second tip flush of 1940 and show a reduction of one growth layer from 2-14-b.

Con T 2-16 (1941-1944)

- a. 3 sce + 1 d arc + inc—6 tfs—3* years.
- b. 3 sce + 2 d arcs + inc—6 tfs—3* years.

Con T 2-16 includes only the first tip flush of 1941.

Con T 2-11 (2d 1941-1944)

- a. 3 sce + 1 dce + 4 d arcs + inc—5 tfs—2½* years.
- b. 2 sce + 1 dce + d arcs + inc—4 tfs—2* years.
- c. 2 sce + 1 dce + d arcs + inc—4 tfs—2* years.
- d. 2 sce + d arcs + inc—3 tfs—1½* years.
- e. 1 sce + inc—2 tfs—1* years.
- f. inc—1 tf—1 year.

Con T 2-11-a, from the second tip flush of 1941, actually contains more growth layers than does 2-16-b. The plus sign with the number of years growth refers to that portion of 1944 from the start of growth to May 22, an interval during which an incomplete growth layer was formed. The localized occurrence of certain growth layers exists in the trunk and thus resembles the same feature in branches.

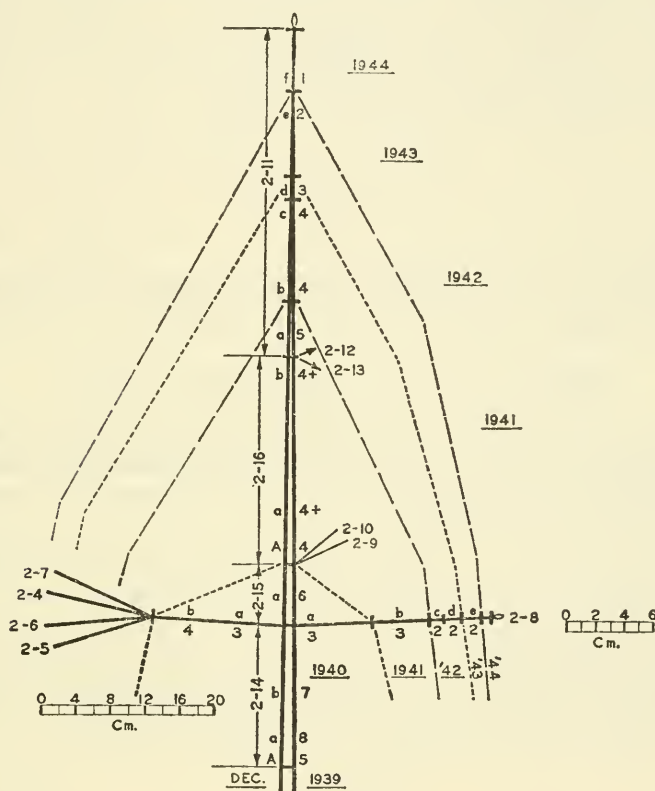


FIG. 51.—Leader of *Pinus taeda* (Con T 2-14 to 2-16, and 2-11) with branch, Con T 2-8, to show annual increase in diameter flushes and tip flushes. Cross-bars represent terminal bud scale scars. Capital letter refers to unstained block removed from leader at early part of 1940 growth. Small letters refer to position of stained sections. Figures opposite the letters give the number of growth layers in the sections represented by the letters. Larger scale for branch 2-8 only.

Much work remains to be done in the task of tracing growth layers from the branches down the length of the trunk and in determining their characteristics. However, all the information so far available indicates that there is no difference between branches and trunk. It is possible that the trunk may have slightly less multiplicity and more subdued localization of growth layers than the branches, but at present such is not borne out by our observations.

VIII. SUMMARY

DISCOVERY OF ABSOLUTE DATING

The discovery of absolute dating by means of natural frost effects opened the way to a study of tree growth, especially in reference to the place and time of cambial activity. The formation of partial growth layers is linked directly to the locality on the tree body where cambial activity occurs; this belongs properly to the subject "Classification of Growth Layers." Subdivisions within the annual increment are linked directly to the time of cambial activity; this belongs to the subject "Multiplicity of Growth Layers."

The possibilities opened up by the discovery that natural frost effects could be used to date annual increments with exactness led directly to the observations, measurements, and experiments reported upon in the present work.

Soon after natural frost effects were put to chronologic use, artificial freezing was introduced as a second potent method of absolute dating.

TREES, LOCALITIES, AND ENVIRONMENTS

Some 36 different species, including both gymnosperms and angiosperms in nearly equal numbers, were brought under study at one time or another. However, work was concentrated on members of the two genera, *Cupressus* and *Pinus*.

Although most of the work was done on trees on the extreme lower forest border in and near Lubbock, Tex., trees from a wide range of moisture, temperature, and length of growing season were measured and sampled at different times. Types of environment varied from that of Yuma, Ariz., to that of the upper timber line in New Mexico and the Appalachian Piedmont of Maryland.

METHODS

The results obtained from observation, measurement, and experiment furnished the bases for the present report. Fieldwork preceded preparation of specimens and microscopic analysis of stained thin sections, out of which emerged a picture of growth layers described under "Classification" and a resolution of the complexities of the annual increment as described under "Multiplicity."

Attention was concentrated upon the branches of trees except for eight trunks which were dissected in whole or in part in order to determine whether or not features typical of branches also characterized the trunks.

With the exception of methods of absolute dating, other methods used were those more or less common to botanical techniques.

DATING CRITERIA

The discovery that growth layers could be dated with exactness by the incidence of natural frost injury and recovery led directly to an intensive inquiry into where and when growth occurs. Altogether four methods were used to date growth layers: Natural frost effects, artificial frost effects, periodic tip-growth measurements, and the relation of tip growth to diameter growth. Materials used herein have been dated absolutely unless otherwise noted.

CLASSIFICATION

The common idea of tree rings pictures them as concentric circles of about equal width on the two-dimensional face of a cross section. This picture is accurate for certain environments but cannot be rationalized for all environments. As a matter of fact, investigation reveals that a ring is merely a cross-section view of a sheath, or layer, of wood which more or less entirely covers the plant body, branches, trunk, and roots; that growth layers may be entire or partial; that partial growth layers may cover either minute fractions of the plant body above ground or nearly all of it; and that partial growth layers may include a variety of types which grade into each other longitudinally and tangentially.

Investigation also reveals that growth layers may vary radially; that the outer border of densewood may terminate abruptly against the succeeding lightwood or may grade outward through a complete transition from densewood into lightwood; that growth layers may be either complete or incomplete radially by the presence or absence of densewood; and that growth may cease without the formation of densewood.

Finally, investigation indicates that the growth processes of cambial activity, differentiation, and maturation may be highly localized on the plant body; that these growth processes are rhythmic and are not of necessity visibly recorded; and that physiological activity modified by environmental influences leaves a more or less detailed record in the xylem.

An interval of physiological activity has been termed a growth flush. If such activity produces xylem, it is called a growth layer. Specifically, a growth layer includes the xylem laid down during a single interval of activity, regardless of where within the plant body the activity occurs, or when.

Evidence thus suggests that cambial activity, differentiation, and maturation begin locally on the aerial plant body, spread out, more or less, and cease. Incipient flushes of growth, in other words, give rise to partial growth layers and, unless prohibited, will ultimately spread into an entire sheath of xylem covering the aerial plant body. This sheath will continue to increase in thickness until growth factors cease to be favorable.

MULTIPLICITY

The subject of multiplicity adds the time factor, with emphasis, to the types and classes of growth layers included under the subject of Classification. Growth may be localized not only in place but also in time.

Investigation reveals that growth may cease at any time after it begins and may be reinitiated at almost any time after it ceases; that the amount of xylem may be limited to a few cells only or may include a layer over the entire aerial plant body; that growth rhythms are not necessarily geared to an annual cycle; that one or several flushes may be recorded by xylem in one year; that the growth layers resulting from intra-annual flushes may, and commonly do, possess outer borders indistinguishable from the borders terminating the annual increment; and that a partial growth layer does not represent an annual increment except for one percent or less of the several thousand partial growth layers that have been dated with exactness.

The studies included under Multiplicity emphasize the fact that growth flushes, and the intervals between them, are distinctly variable in length.

A merging of the results obtained from studies of Classification and Multiplicity indicates the place, the time, and the intensity of a growth flush. The visible result of a growth flush is one of the many varieties of growth layers. Thus, we may define a growth layer as follows: It includes the xylem laid down by the cambium during a single period of activity regardless of entirety around the circuit, of completeness radially, of location within the plant body, or regardless of the particular time of the activity.

As a matter of fact, growth processes are predominantly and intricately rhythmic—they may leave traces of themselves in the xylem which are, so to speak, invisible as well as visible.

IX. CONCLUSIONS

The discovery and use of absolute dating offer a unique opportunity to trace in some detail the history of growth flushes, and to determine

the amplitude and the wavelength of growth activity provided its intensity is plotted against time. The physiological activity of a growth flush, no matter where and when intensified, produces a growth layer, entire or partial, complete or incomplete.

Our work on trees grown under extreme lower forest-border conditions and in the forest border itself shows that multiple flushes within one year can, and do, yield multiple growth layers within an annual increment. From the forest interior, where it is thought that an annual increment seldom if ever contains multiple growth layers, out to the forest edge and into the scattered trees beyond, the tendency toward and the presence of multiplicity increase until it becomes of high order as illustrated by the trees studied in the present report. The error in the simple counting of sharply bounded growth layers, interpreting them to be annual, is therefore rather large among trees grown under extreme forest-border conditions. Within the true forest border as commonly understood, where conditions are more favorable to tree growth than at Lubbock, Tex., the range of this error is estimated to be from zero to 15 percent, the average error being about 5 percent.

It is abundantly clear, therefore, that growth rings cannot be used for precise dating of historical events if the trees grew in or near the forest border. A tree-ring calendar centuries in length, from the lower forest border, would, it is believed, have its accuracy enhanced for purposes of archeological dating if it contained numerous "bench marks" or check points, if it could be duplicated by other materials or records, or if it could be duplicated by other students. Even so, errors due to indistinguishable intra-annual growth layers could not be wholly eliminated.

It is also abundantly clear that growth-layer sequences from forest-border areas, where multiplicity is characteristic, cannot be used for precise rainfall or cycle studies. The reasons are quite obvious.

Although growth layers from forest-border trees do present difficulties in chronological reckoning, it must be remembered that all trees, whether from the forest border or forest interior, require soil moisture and that many of them must meet the problem of soil-moisture deficit.

In spite of possible chronological difficulties, growth layers may be used in an analysis of environmental factors in at least two ways: (1) by selecting trees that have grown under conditions where the annual cycle of growth is seldom broken into secondary cycles, that is, trees grown toward the interior and away from the lower forest border, and (2) by analyzing growth patterns. The chief gross elements in a pattern are multiplicity (or its absence), partial growth layers, vari-

ability of sequence, and relative and absolute thicknesses. Patterns vary under different types of rainfall and different soil-moisture regimes (Glock, 1955b).

Strong evidence indicates that the trunk of a tree duplicates the history and vicissitudes of growth as written in the branches. Of course, the story in the trunk is continued longer and is perhaps more synoptic in nature. Branches were studied to a great extent in the present work not only because of the obvious advantage in manipulations and measurements but also because their growth layers could be dated in absolute fashion. If, by chance, branches carry a more complete record of fluctuations in physiological activity than the trunks do, then the study of branches becomes of great ecologic importance.

It is hoped that the present work will in some measure contribute to a better understanding of tree growth, especially in the lower forest border of southwestern United States, and that it has answered to some extent the questions stated in the introduction. There remains the task of applying the methods of exact dating, as defined herein, to tree growth along a transect from the lower forest border into the forest interior. An investigation of the fundamentals of tree growth at the forest interior stands out as a desideratum of high order. When does growth occur at the interior? Where on the plant body does growth occur? Are partial growth layers ever found in normal trees at the forest interior? These and other questions await analysis of growth under the discipline of exact dating. Not only forest interiors but also other forests, other forest borders, and other species, wherever they may be, await patient investigation with promise of decisive and perhaps unexpected results.

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PLATES

PLATE I

Fig. 1. *CMP 1-1-b*. Branch section of *Pinus cembroides*, cut January 3, 1941. Xylem probably of 1937-1940. Normally developed growth layers in a pine; probable natural frost injuries in 1938 and 1940; incipient visible growth rhythm and initial departure from unity in 1940. Compare with plate 3, figure 2.

Fig. 2. *CMJ 1-1-a*. Branch section of *Juniperus pachyphloea*, cut January 3, 1941. Xylem of 1937-1940. Intimate relation between frost injury of 1938 and dw*; bifurcation of annual densewoods and contrast of outer densewoods of annual increments.

1937: multiple dw; sce.

1938: msce connected with frost injury, dw filling gaps in discontinuous circle of injury and following outward the injury effects themselves; msce whose dw spreads into a curtain effect giving diffuseness, then changes to sL.

1939: 2 sce, outer dw with ddw which changes tangentially to sL.

1940: sce.

* For explanation of abbreviations, see page 101.

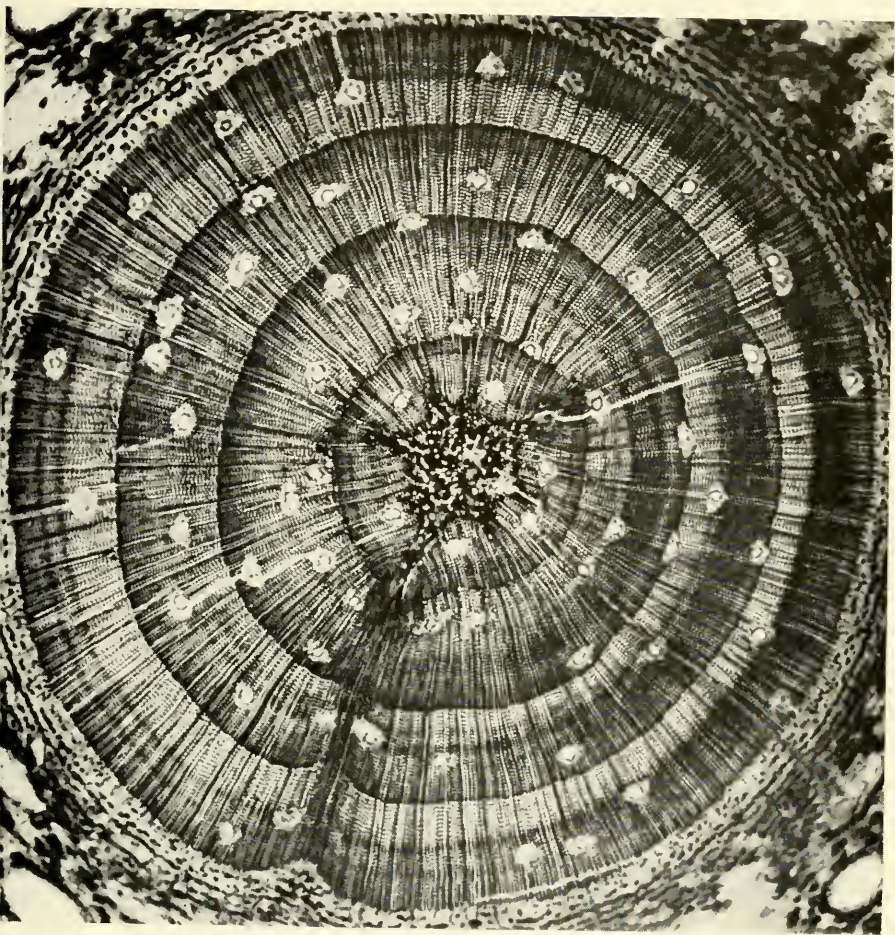


FIG. 1.

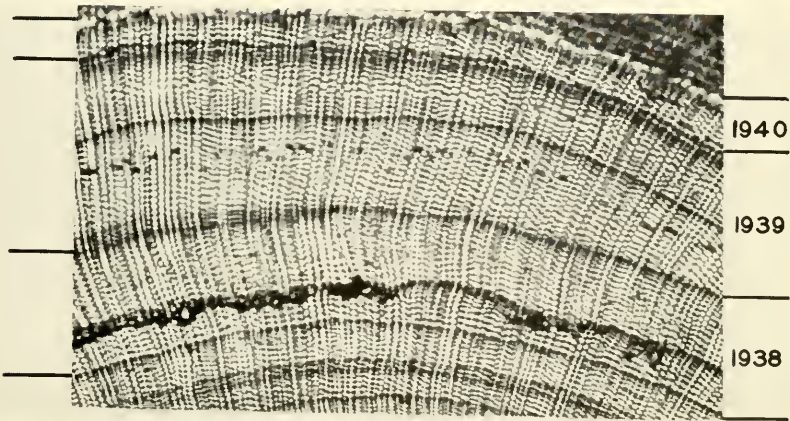


FIG. 2.

PLATE 2

Fig. 1. *Con T 2-o-base b 1*. Trunk section of *Pinus taeda*, cut May 18, 1944, at 17 cm. above ground and 228 cm. below base of terminal bud (146 cm. below base of bud as of December 1939). Xylem of 1939-1942. Absolute dating based upon effects of artificial freezing (of April 5, 1940) and date of cutting section; contrast of densewoods terminating annual increments which show great variation in definition.

1939: Very weak dw.

1940: Artificial frost injury and recovery some 8 cells out; outer dw weak, diffuse, almost nonexistent giving complete subsidence of annual character of the "ring."

1941: Outer dw thick, heavy, sharp, striking contrast to outer dws of 1940 and 1939; outer dw has slight evidence of ddw.

1942: A dce as ilw; see with wide ddw.

Fig. 2. *Con T 2-o-base b 1*. Enlarged portion of figure 1 (above). Xylem of 1939-1941. Artificial frost effects and breakdown of outer marginal definition of annual increment; absolute dating.

1939: dw weak, subdued, 1 cell thick.

1940: 7-10 cells, as reversed sequence, laid down radially by April 5, 1940, when artificial freezing was applied; artificial frost injury and recovery; outer dw thin, highly diffuse and essentially nonexistent on some radii.

Fig. 3. *Con T 1-12-a*. Branch section of *Pinus taeda*, cut January 16, 1943, from first 1940 tip flush. Xylem of 1940-1942. Absolute dating by periodic tip-growth measurements; proved multiplicity by 4 growth layers for 4 tip flushes for 3 years; normally developed growth layers with tendency toward growth rhythms by ilw's; densewoods a bit weak; nuclei visible.

1940: 2 sce; outer gl with diffuse arcs or ilw.

1941: 1 sce with ilw.

1942: 1 sce with ilw and idw.

Rhythms expressed by ilw and idw are taken to be incipient departures from strict unity in the gls of an annual increment.

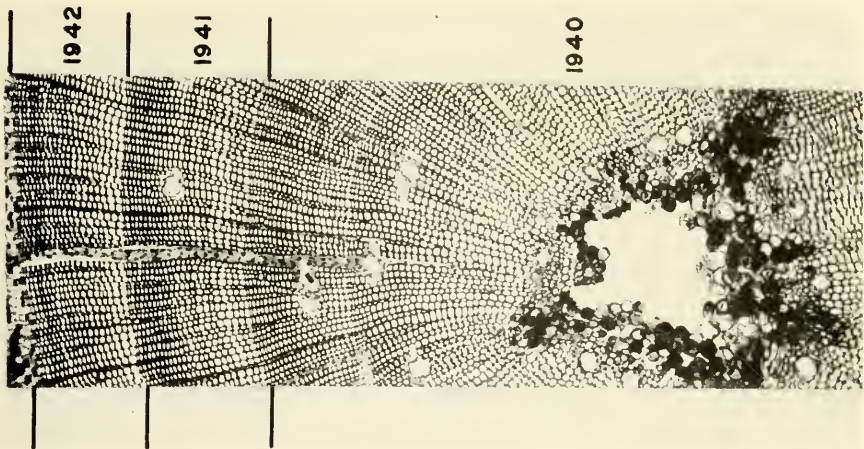


FIG. 3.

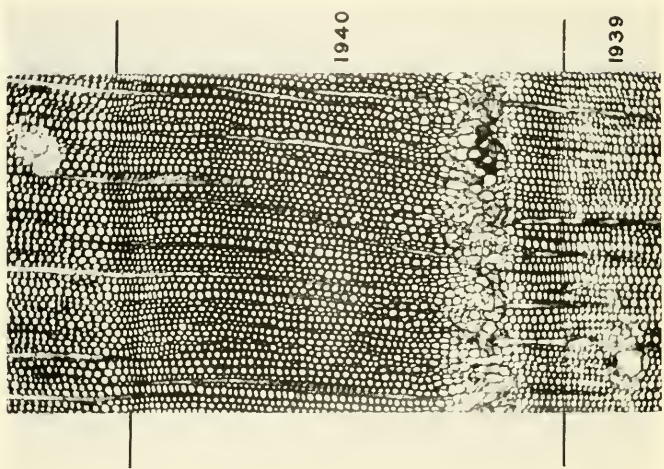


FIG. 2.

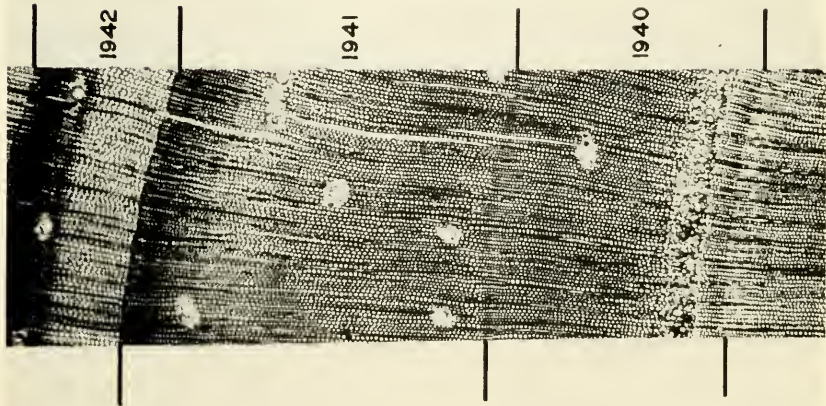


FIG. 1.

PLATE 3

- Fig. 1. *SA 1-a*. Stem section of shrubalthea, *Hibiscus syriacus*, cut October 28, 1939. Xylem of 1933(?) - 1939. Ring-porous angiosperm grown on a lawn and watered periodically. Natural frost injuries in 1936 and 1938; partial gls; dw intermittent radially; "invisible" dw.
- 1933 (probably): are with invisible extension both directions tangentially; see.
- 1934 (probably): Compound lens with intermittent dw and nearly "invisible" dw; see.
- 1935 (probably): Thick lens with intermittent and invisible dw; see.
- 1936: Frost injury; thin sL; see.
- 1937: see.
- 1938: Frost effects; see with intermittent dw.
- 1939: Thin see.
- Densewoods, whether intra-annual or annual, are intermittent tangentially.
- Fig. 2. *TRP 1-1-a*. Branch section of *Pinus aristata*, cut June 28, 1942. Typical growth layers in a bristlecone pine; thick and thin densewoods. Multiplicity suggested by ilw one cell thick in 3d gl, and by presence of 13 diameter flushes for 12 tip flushes (probable multiplicity in north-central New Mexico at 9,000 ft. on a dry, steep, rocky slope). Elsewhere on section, 1942 growth represented by lenses of immature cells; in this case, therefore, diameter growth preceded tip growth, of which there had been none up to June 28.

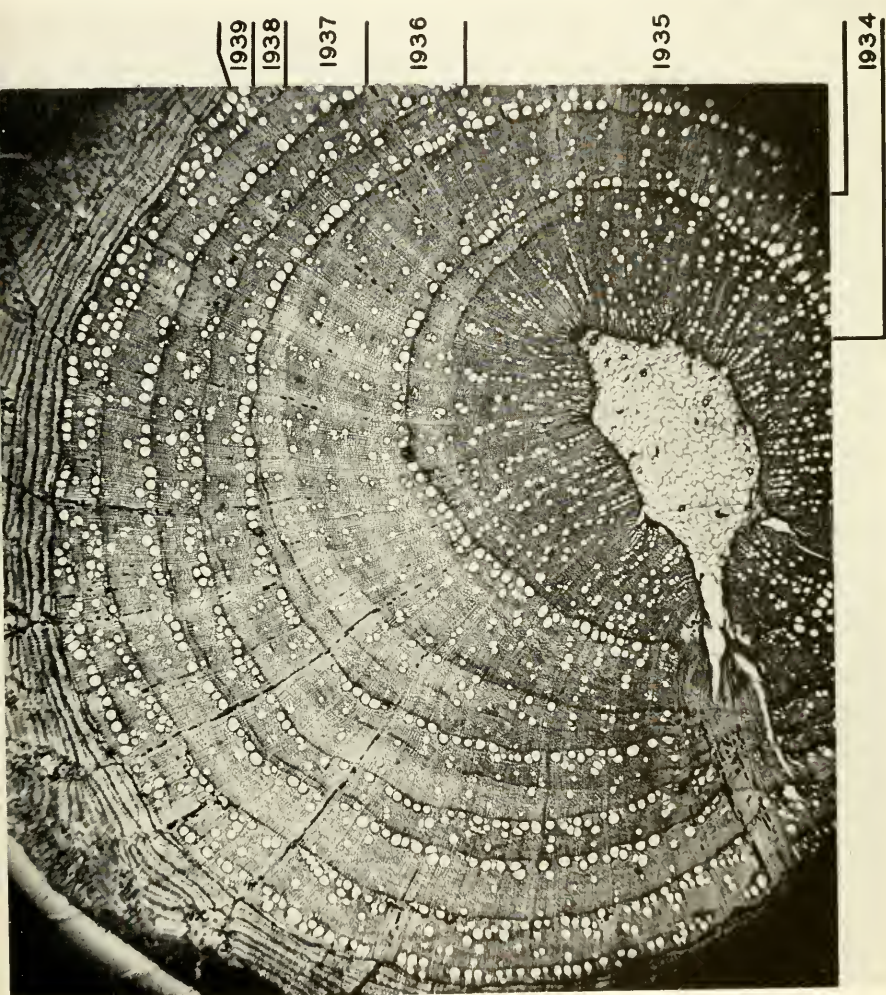


FIG. 1.

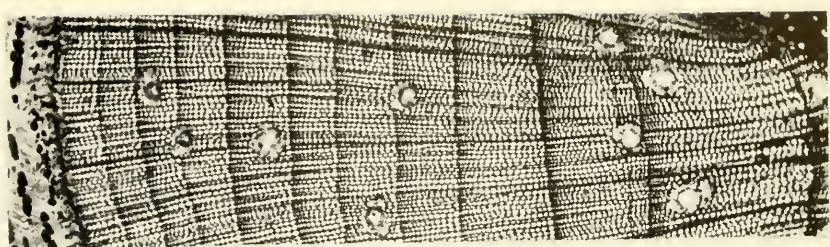


FIG. 2.

PLATE 4.

- Fig. 1. *TtAp 2-1-a*. Branch section of *Malus sylvestris*, cut April 21, 1940. Xylem 1938-1940. Natural multiplicity and multiplicity caused by irrigation; intra-annual dw more definite than annual.
1938: 2 sce, inner thick, outer thin.
1939: 2 sce, inner thick, outer thin and induced by 4-inch irrigation of July 25, 1939.
1940: Growth to April 21.
- Fig. 2. *TTC 1-10-a*. Branch section of *Cupressus arizonica*, cut April 21, 1940. Sequence probably of 1938-1940. Irregular outer margins; facing half lenses; growth to April 21.
1938: Circle of parenchyma cells; ddw; ce gl with irregular outer margin.
1939: Possible frost spot; arc of parenchyma cells; waves of highly lignified cells; 2 facing $\frac{1}{2}$ L's, sharp at cusps, diffuse away from cusps; fading dw, nonexistent dw or invisible margin; $\frac{1}{2}$ L's disappear within 16 cm. outward on branch; ce gl with irregular margin.
1940: Growth to April 21; 8 to 16 cells, immature on short radius, largely lignified on long.

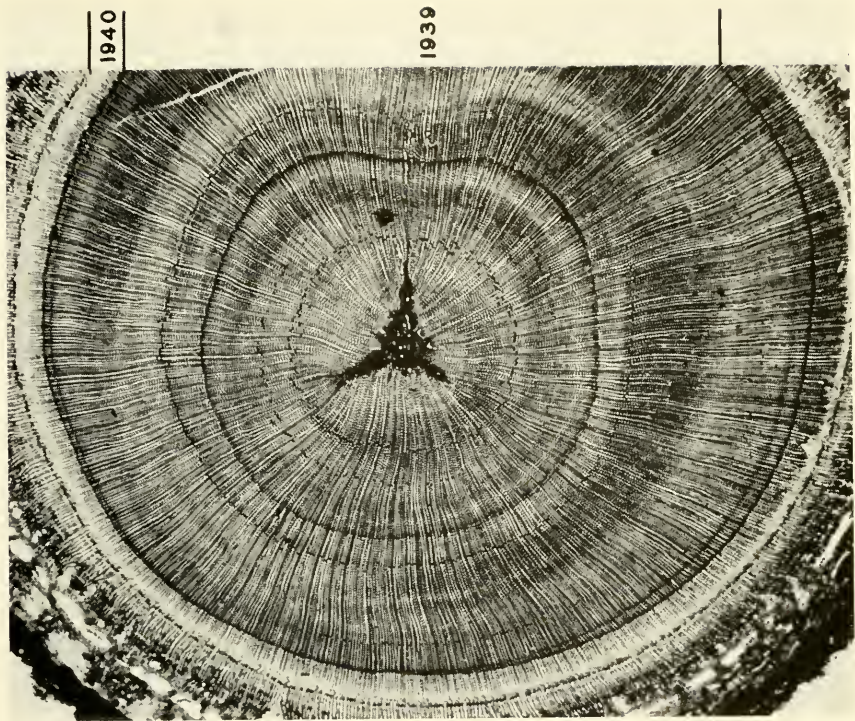


FIG. 2.

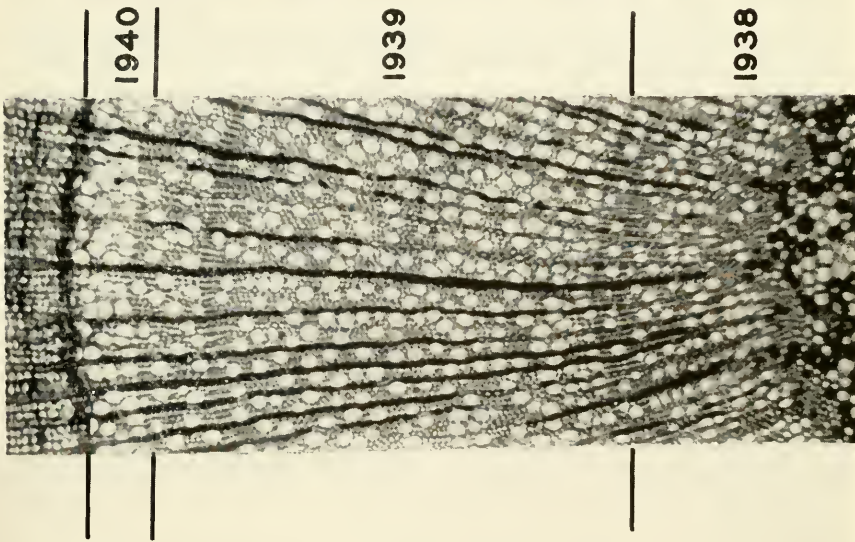


FIG. 1.

PLATE 5

Fig. 1. *TTC 1-11-a*. Branch section of *Cupressus arizonica*, cut November 24, 1945. Xylem of 1938-1945. Bridge between natural frost effects of 1938 and 1945; partial growth layers; sharp and diffuse intra-annual growth layers, elsewhere on the section all but 2 of the annual increments contain sharp lenses.

1938: sce with thin dw.

1939: 2 sce, outer dw the stronger; psL.

1940: 2 dce; sce.

1941: sce with thin dw.

1942-44: Thin sce's with threadlike dw's.

1945: Frost effects; sce.

A comparison of this figure with figure 2 (below) and figure 1 of plate 6, and with figure 2 of plate 6 and figure 1 of plate 7 gives a study in longitudinal continuity along the branch.

Fig. 1, pl. 5—244 cm. from tip of branch.

Fig. 2, pl. 5 and fig. 1, pl. 6—212.4 cm. from tip of branch.

Fig. 2, pl. 6 and fig. 1, pl. 7—77.5 cm. from tip of branch.

Fig. 2. *TTC 1-11-b*. Portion of branch section 31.6 cm. outward on branch from figure 1 (above). Xylem of 1941-1945. Absolute dating by means of natural frost effects in 1943, 1944, 1945. Study in circuit uniformity by comparison with figure 1, plate 6; and longitudinal uniformity by comparison with figure 1 (above) and figure 2, plate 6, and figure 1, plate 7.

1941: sce with incipient ddw.

1942: sce with ddw; sL.

1943: Natural frost effects; sce with added dw cells.

1944: Natural frost spots; sce.

1945: Intense natural frost effects; sce.

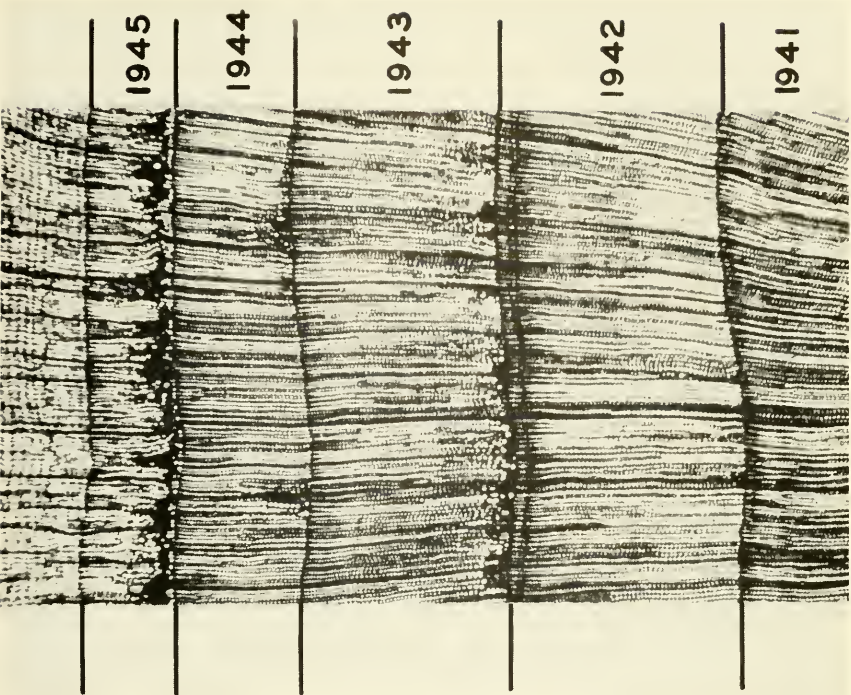


FIG. 2.

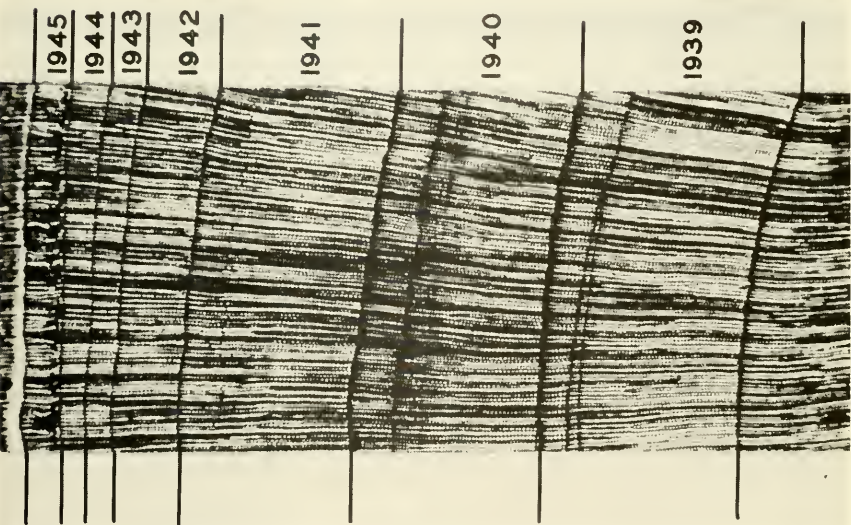


FIG. 1.

PLATE 6

Fig. 1. *TTC 1-II-b*. Portion of same branch section as in figure 2, plate 5, but nearly opposite radius. Xylem of 1941-1945. Dating by natural frost effects. Compare with figure 2, plate 5, for variations around the circuit, with figure 1, plate 5, and figure 2, plate 6, and figure 1, plate 7, for variations along the branch. Partial growth layers and multiplicity.

1941: sce; ddw as an incipient growth layer.

1942: dL's; psL, sce.

1943: sL; sce.

1944: Natural frost spots; 2 sL as compound lens; sce.

1945: Natural frost circle; sce with ddw.

Fig. 2. *TTC 1-II-d*. Portion of a branch section 134.9 cm. outward on branch from figure 2, plate 5, and figure 1, plate 6. Xylem of 1941-1945. Dating by natural frosts here and elsewhere on circuit. Compare with figure 1, plate 7, for variations around circuit, with figure 2, plate 5, and figure 1, plate 6, and figure 1, plate 5, for variations along branch. Lensing and weak annual boundaries.

1941: sce with ddw and irregular outer margin.

1942: sce with weak dw.

1943: s $\frac{1}{2}$ L; sce with very thin, weak dw after separation of $\frac{1}{2}$ L.

1944: Spots of natural frost effects; sL; s $\frac{1}{2}$ L diffusing into an incipient "invisible" gl; sce.

1945: Natural frost circle; sce with irregular dw.

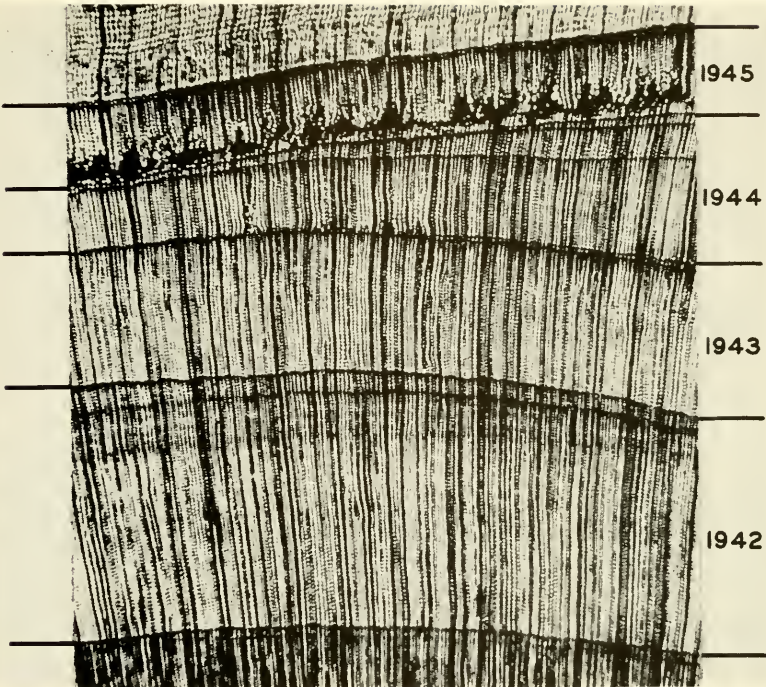


FIG. 1.

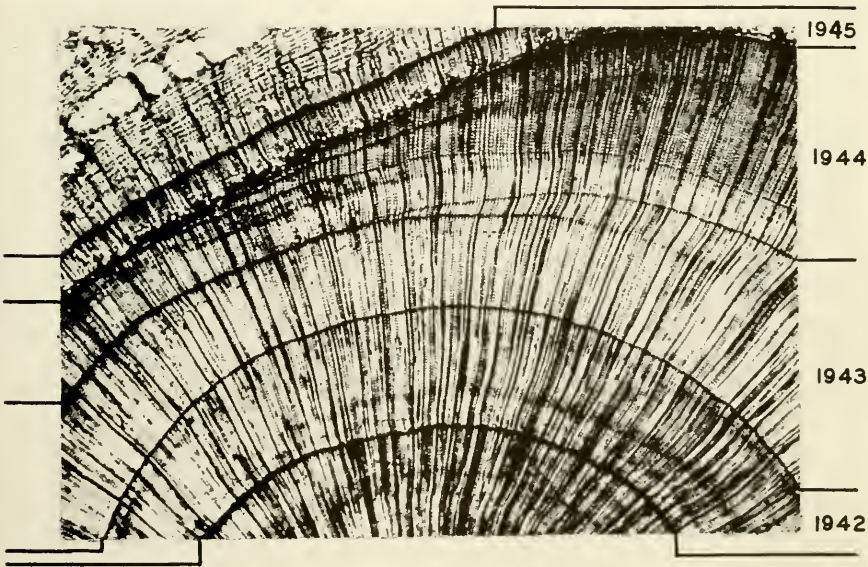


FIG. 2.

PLATE 7

Fig. 1. *TTC 1-11-d*. Portion of same branch section as in figure 2, plate 6, but on nearly opposite radius. Xylem of 1943-1945. Dating by natural frost effects. Compare with figure 2, plate 6, for variations around circuit, with figure 2, plate 5, and figure 1, plate 6, and figure 1, plate 5, for variations along branch. Lensing in opposite directions in successive annual increments; weak annual dw.

1943: see with weak dw.

1944: Natural frost spots; lenses opening to left; see, but at right, outer dw of increment is weak and 1 cell thick.

1945: Natural frost circle; lens opening to right; see with irregular outer margin.

Fig. 2. *TTC 5-10-a*. Branch section of *Cupressus arizonica*, cut February 1, 1941. Parts of 1939 and 1940 increments. Lens under high power showing lenticular lightwood and continuous densewood.

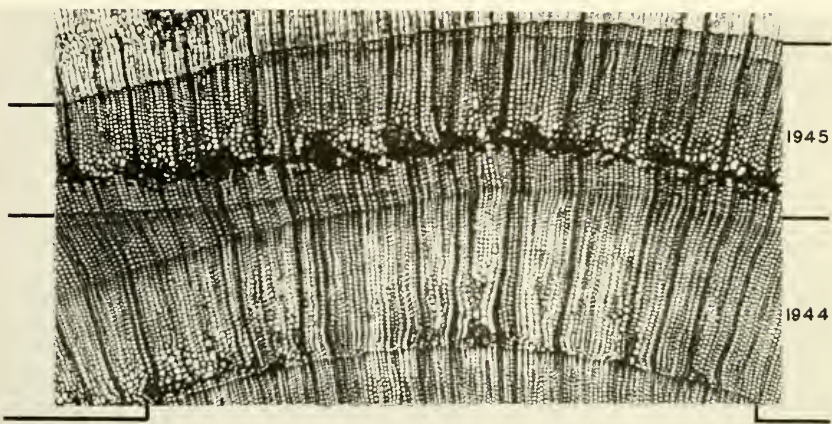
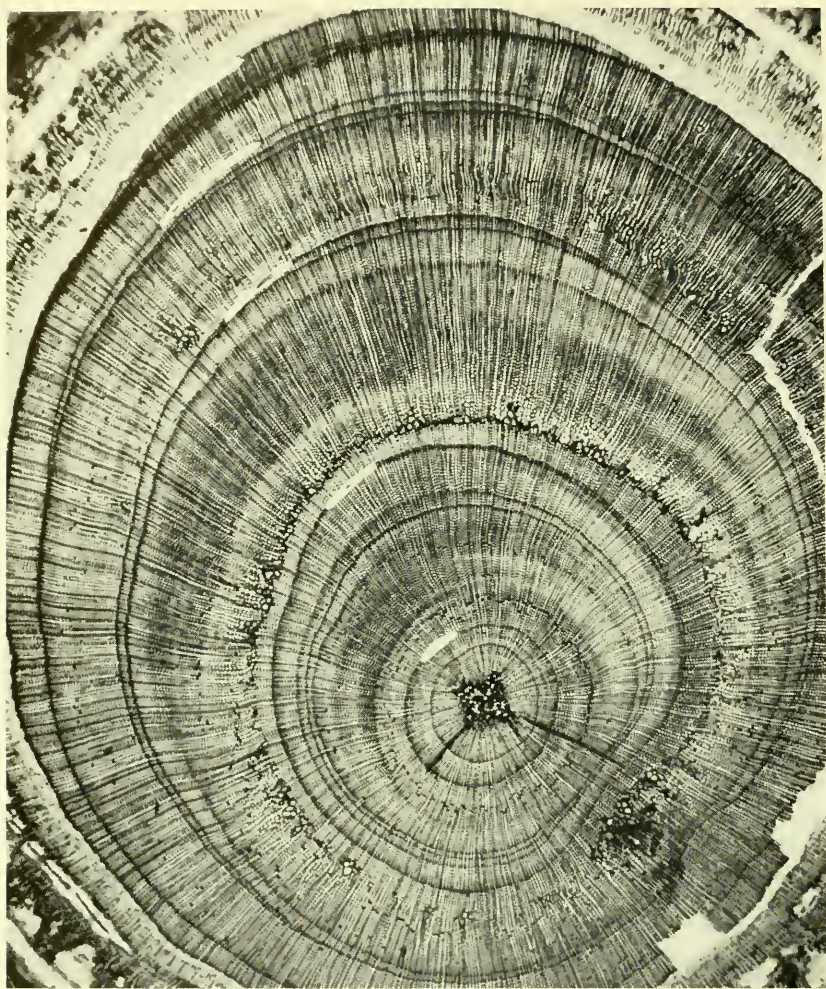


FIG. 1.



FIG. 2.



TTC 5-11-a. Branch section of *Cupressus arizonica*, cut April 5, 1941. Xylem of 1936-1941. Dating by natural frost effects; single and compound lenses; multiplicity by partial and entire gls; transition between ddw and sharp lenses; rhythmic dw.

1930: 2 sce, inner dw slightly the sharper.

1937: psL; sce; msce; sce with ddw and irregular outer margin.

1938: Typical effects of natural frost; psce with sharp, diffuse, and invisible margin; long msL; sce; short sL.

1939: Natural frost spots; sce; sharp compound lens.

1940: Natural frost spots; sce with multiple ddw (or 2 sL's) and irregular outer margin; sL.

1941: inc. lens.

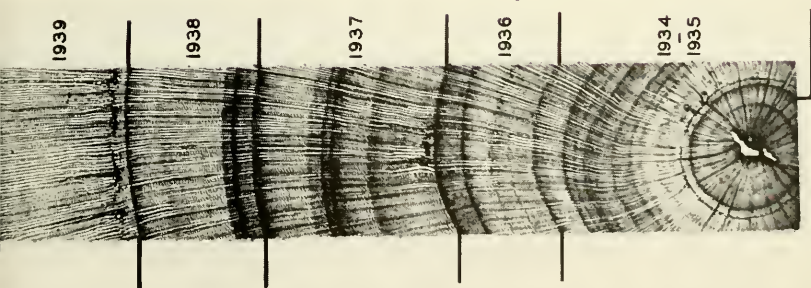


FIG. 1.

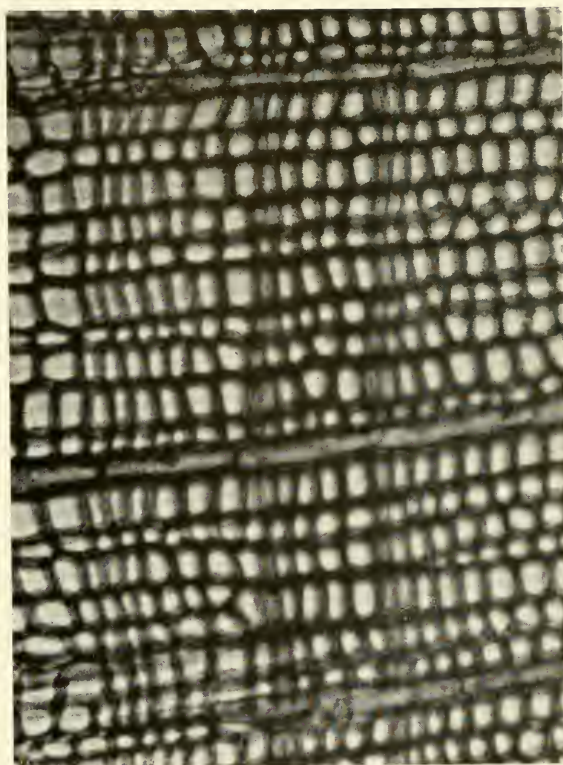


FIG. 2.

(See legends on following page.)

PLATE 9

- Fig. 1. *TTC 12-9-b*. Branch section of *Cupressus arizonica*, cut February 29, 1940. Xylem of 1933(?) - 1939. Dated multiplicity; curtains.
1933: psce, sce.
1934-35: Natural frost circle; several psce; 3 sce.
1936: Natural frost spots; 2 sce.
1937: Natural frost spots; psce; msce; sce; msce curtain; sce. (See fig. 2, below, for detail of curtain.)
1938: Thin sce; sharp curtain grading into psce; sce.
1939: Circle of natural frost effects; sce.
- Fig. 2. *TTC 12-9-b*. Detail of mid-1937 on figure 1, above. A thick gl with thin dw, a thin gl, and a thin gl with poorly developed dw giving a curtain effect to the preceding gl.

PLATE 10

- Fig. 1. *TTC 12-12-b*. Branch section of *Cupressus arizonica*, cut July 31, 1944. Xylem of 1943-1944. Multiplicity proved by tip-flush measurements; ddw and initiation of lensing.
1943: sce (at center); psce with psL; sce with ddw.
1944: msce with ddw grading into lens and with intermittent densewood; sce probably; inc L's.
- Fig. 2. *TTC 12-14-b*. Branch section of *Cupressus arizonica*, cut November 17, 1945. Xylem of 1942-1945. Outer margin of xylem made irregular by a striking example of psg; thread of ilw; thin dw; idw.
1942: sce with irregular outer contact suggesting outer margin of 1945.
1943: ilw well out in lw and just under dw; sce with thin dw and with hint of idw.
1944: Suggestion of ilw; sce with thin dw.
1945: Thin sce with thin dw; well-lignified psg in patches. (See fig. 1, pl. 11, for detail.)

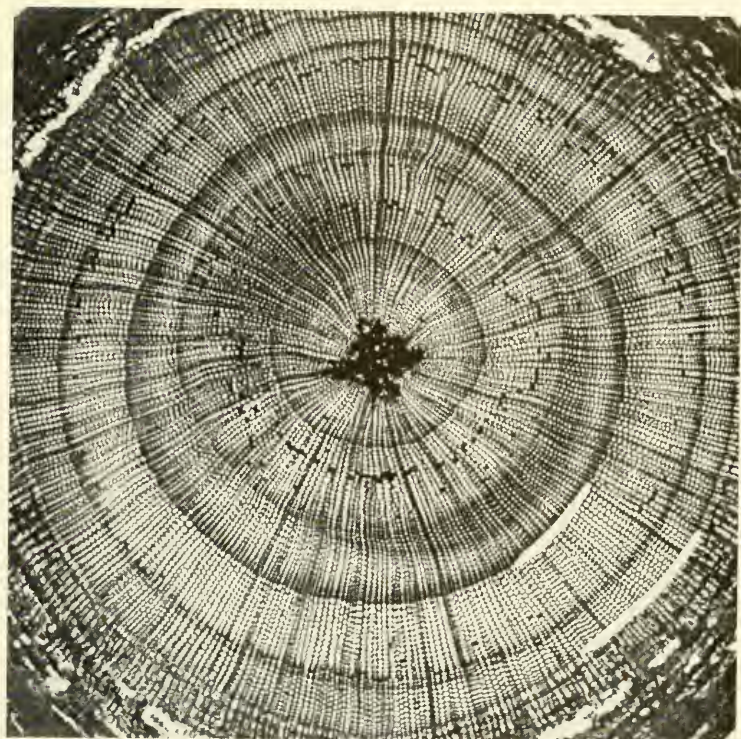


FIG. 1.

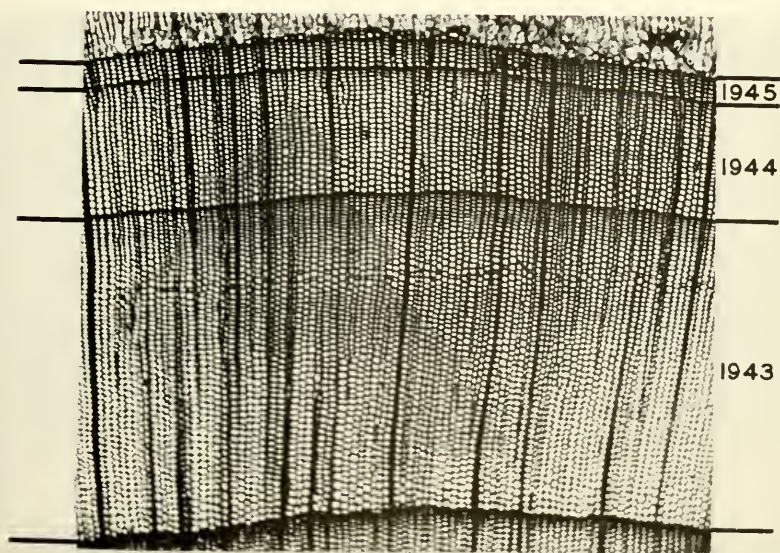


FIG. 2.

PLATE 11

Fig. 1. *TTC 12-14-b*. Detail of figure 2, plate 10. Xylem of 1944-1945. Mature cells as striking example of psg.

1944: see with dw 1-cell thick.

1945: see with dw 1 to 2 cells thick; psg of mature cells added outside the normal 1945 growth.

Fig. 2. *TTC 12-14-c*. Branch section of *Cupressus arizonica*, cut November 17, 1945. Xylem of 1943-1945. Dw 1-cell thick; dw which resembles ilw.

1943: see whose dw is 1 to 2 cells thick.

1944: see with 2 lw cells and 1-2 dw cells. Dw appears to be ilw attached to 1945.

1945: see with irregular outer margin; scattered mature cells of psg.

Fig. 3. *TTC 30-1-b*. Branch section of *Cupressus arizonica*, cut November 4, 1939. Xylem of 1939. Annual increment with indefinite margin, indefinite dw, and psg. Incipient dw (poorly developed and diffuse) followed radially by large nucleated immature cells, the psg. Had this branch grown another year before sectioning, one would have difficulty in determining the outer margin of 1939 growth.

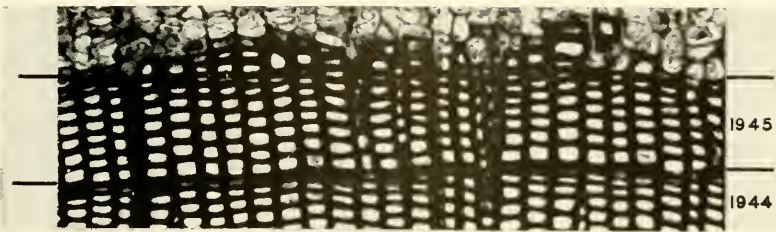


FIG. 1.

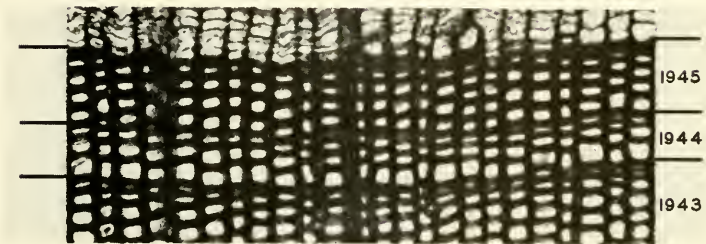


FIG. 2.

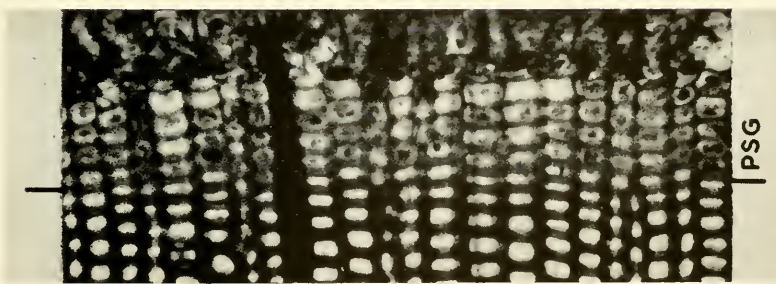


FIG. 3.

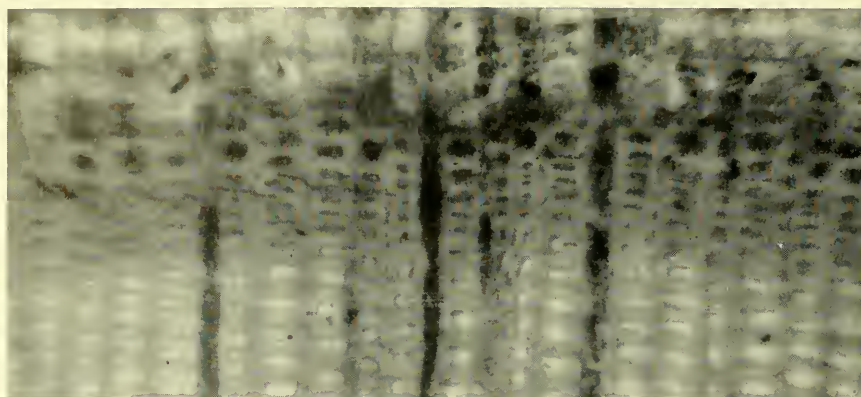


FIG. 1.

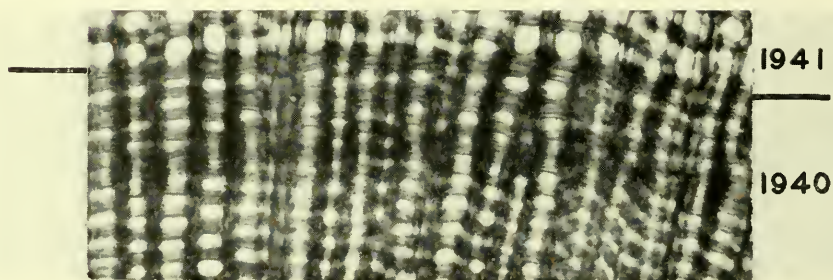
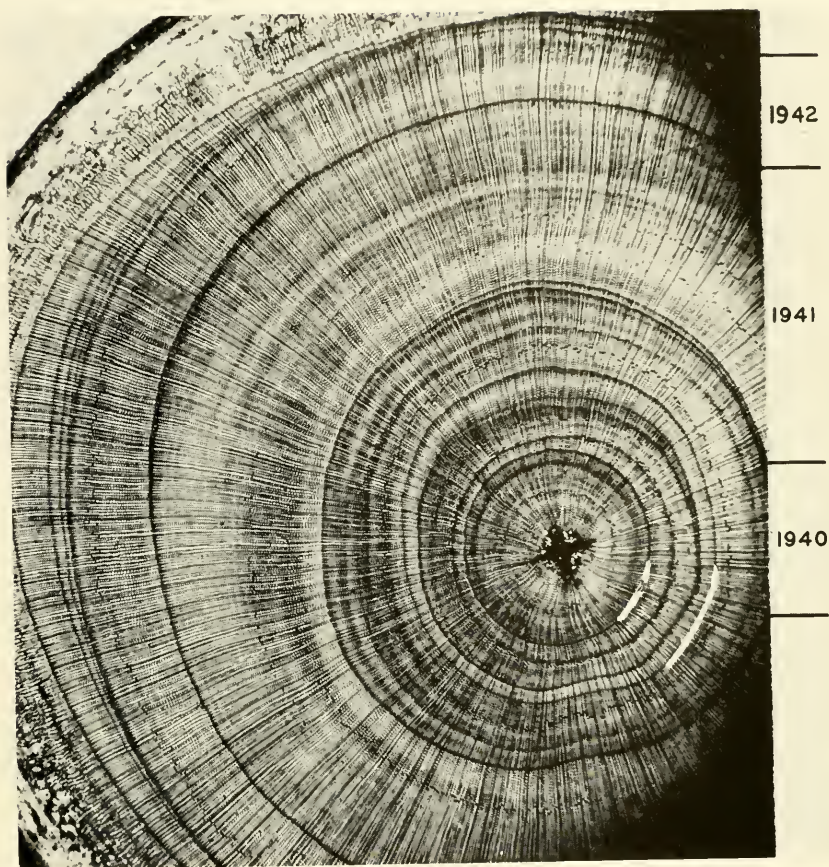


FIG. 2.

Fig. 1. *TTC 33-10-b*. Branch section of *Cupressus arizonica*, cut January 1, 1943. Xylem of 1942 only. Densewood followed by postseasonal growth whose cell columns extend variable distances into cambial region. Outer margin of xylem is irregular and annual margin of growth layer would have been diffuse if growth had been permitted to continue.

Fig. 2. *TTC 33-11-a*. Branch section of *Cupressus arizonica*, cut January 1, 1943. Xylem of 1940-1941. Multiple divided densewood in outer dw of 1940 annual increment. A first step in lens formation by a brief episode of cell enlargement and perhaps a brief interval of variation in cambial activity.



TTC 33-13-a. Branch section of *Cupressus arizonica*, cut January 1, 1943.
 Xylem of 1938-1942. Lensing simple, exterior, compound, and overlapping;
 multiplicity; growth rhythms.
 1938: dce; sce.
 1939: Frost connected msce; dL; sce; outer thin sce.
 1940: Growth rhythms (1938-41); dL; sce; sL.
 1941: sce; ddw as incipient lens.
 1942: sce; compound and overlapping lens of 4 members.

PLATE 14

Fig. 1. *TTC 34-3-a*. Branch section of *Cupressus arizonica*, cut November 29, 1941. Xylem of 1936-1941. Typical natural 1938 frost; sharp lenses; weak densewood under cambium.

1936: dce; sce.

1937: Circles of parenchyma cells; injury; sce.

1938: Circle of natural frost effects; sce with weak densewood.

1939: sce; sL.

1940: sce and ddw; sL.

1941: sce with weakly developed dw.

Fig. 2. *TTC 34-6-a*. Branch section of *Cupressus arizonica*, cut November 29, 1941. Xylem of 1937-1941. Gradations in marginal definition of intra-annuals, from weak and diffuse (1938) to strong and sharp (1939); outer thin growth layer.

1937: sce.

1938: Circle of natural frost effects; dce; sce.

1939: Parenchyma circle; sce (contrast with dce of 1938); sce as "outer thin" with weak dw and lenticular lw.

1940: Natural frost effects; bands of diffuse dw; sce; long sL.

1941: sce.

Outer thin of 1939 judged to belong to 1939 because of position of frost effects in 1940. Figure 1, plate 15, gives detail of this figure.

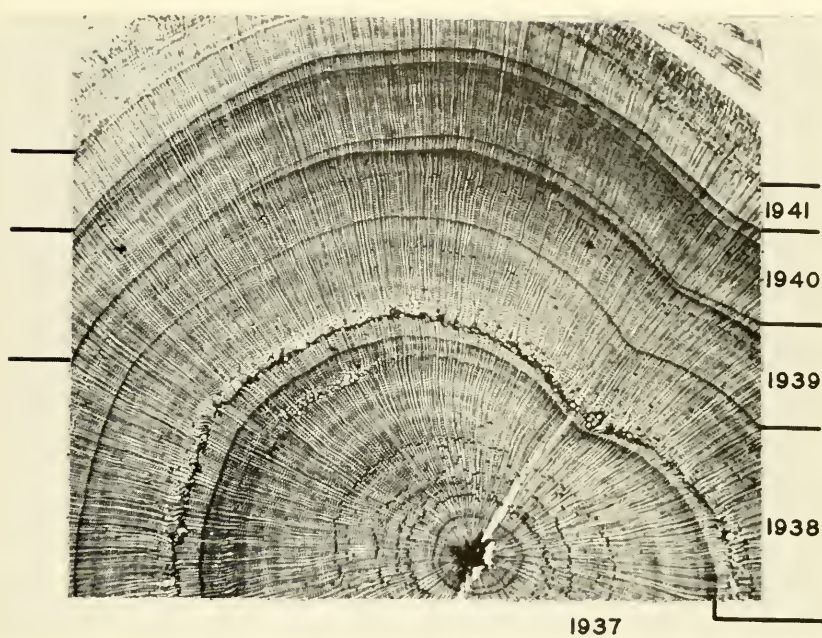


FIG. 1.

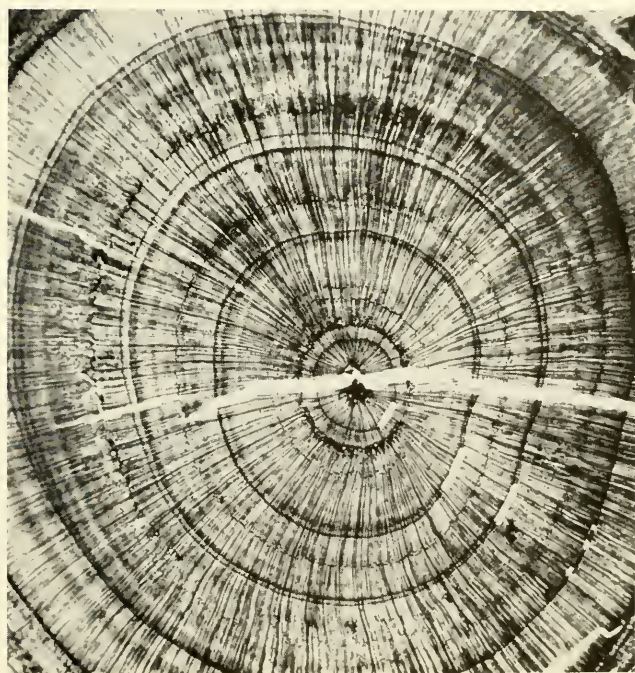


FIG. 2.

PLATE 15

Fig. 1. *TTC 34-6-a*. Enlarged detail of figure 2, plate 14. Xylem of 1939-1941. Multiplicity of gls in annual increments; variation of dw development; "outer thin" gls; intra-annuals indistinguishable from annuals.

1939: 2 sce, dw band of inner gl stronger than dw of annual.

1940: Effects of natural frost; 2 sce, dw band of inner gl nearly the same strength as dw of annual.

1941: sce.

Fig. 2. *TTC 36-5-b*. Branch section of *Cupressus arizonica*, cut January 1, 1943. Xylem of 1940-1942. Dated multiplicity; heavy dw of intra-annual.

1940: Rhythmic dw; 2 sce, inner dw heavy.

1941: Parenchyma circle; faint dce; sce.

1942: 2 sce, dw of inner gl heavier than dw of outer gl, outer contacts of both gls slightly irregular. Elsewhere on section, dw of inner gl splits apart with insertion of lw cells.

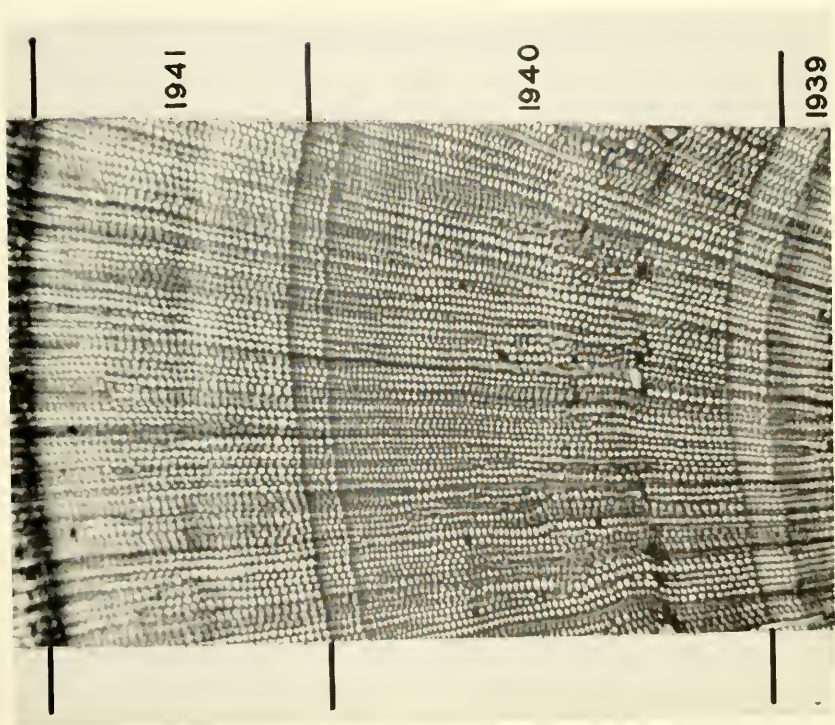


FIG. 1.

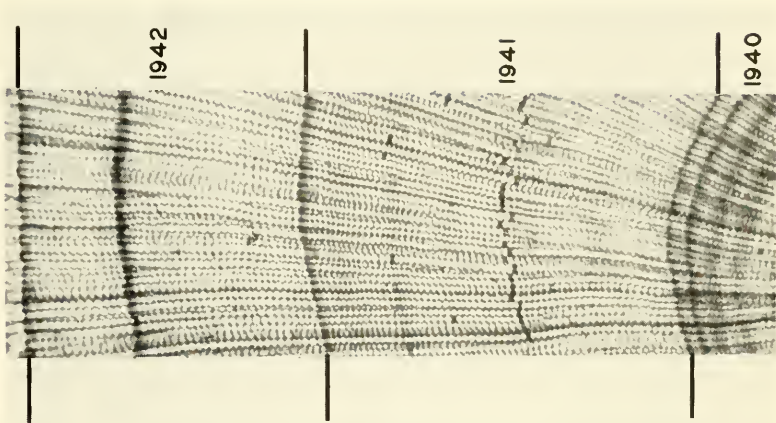


FIG. 2.

PLATE 16

Fig. 1. *TTJ 2-4-a*. Branch section of *Juniperus virginiana*, cut January 1, 1943. Xylem of 1937-1942. Sharp arc; transition between an entire gl and a lens; short diffuse incipient lens.

1937: sce, with outer margin made irregular by "added on," highly lignified cells.

1938: Slight effects of frost injury and parenchyma circle; sce.

1939: Parenchyma circle and dw cells; rhythmic densewood; dce; sce.

1940: sce; "outer thin" sce whose dw is entire and whose lw is entire except over a few degrees.

1941: s arc; short dL, closer to being a lens than ddw; sce.

1942: Faint dL's; sL; sce.

Fig. 2. *TTP 20-6-a*. Branch section of *Pinus ponderosa*, cut February 1, 1941. Xylem of 1939-1940. Irregular and immature xylem under the cambium; single to double row of dw cells as ilw in midst of annual increment.

1939: sce with irregular outer contact.

1940: lw apparently terminated by ilw, which is followed by poorly developed dw; irregular and immature outer border. Actually ilw (or idw) is outer dw of an msce, and the poorly developed dw outside the ilw is an inc L.

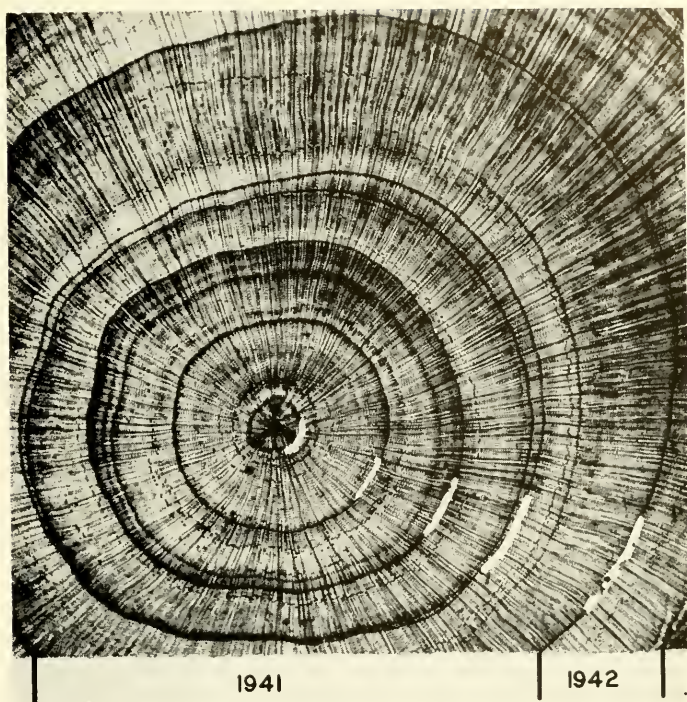


FIG. 1.

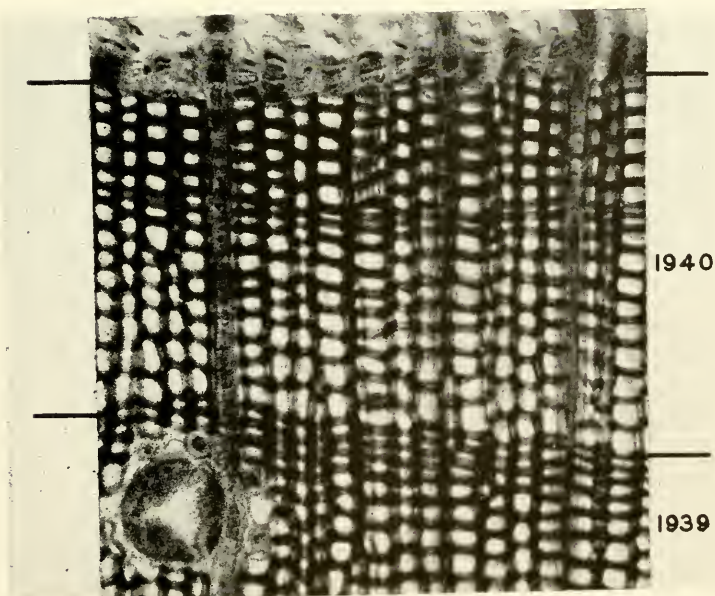


FIG. 2.

PLATE 17

Fig. 1. *TTP 23-2-a*. Branch section of *Pinus ponderosa*, cut November 29, 1941. Xylem of 1937-1941. Proved multiplicity; irregular margin under cambium; lensing; psg.

1937: see.

1938: Slight natural frost effects; see.

1939: msce.

1940: Effects of natural frost; msce.

1941: see; irregular, inc. lenses, as psg, outer tangential walls of outer xylem cells not lignified. Compare with figure 2, below, and figure 1, plate 19.

Fig. 2. *TTP 23-4-c*. Branch section of *Pinus ponderosa*, cut November 29, 1941. Xylem of 1938-1941. Atypical gls; weak dw; weak annual.

1938: see with near normal dw.

1939: Single gl with dw so weak as to be nearly nonexistent.

1940: 3-4 cells thick radially, some radial columns have normal sequence of lw and dw, others all dw; rest all lw (inward on branch 1940 reduced to ddw of 1939 in one or two places and a single row of dw cells elsewhere); under low powers 1940 invisible or present as tiny lenses.

1941: inc. gl; very irregular margin; cambium killed by artificial freezing of May 25, 1941.

Compare with figure 1, above, and figure 1, plate 19.

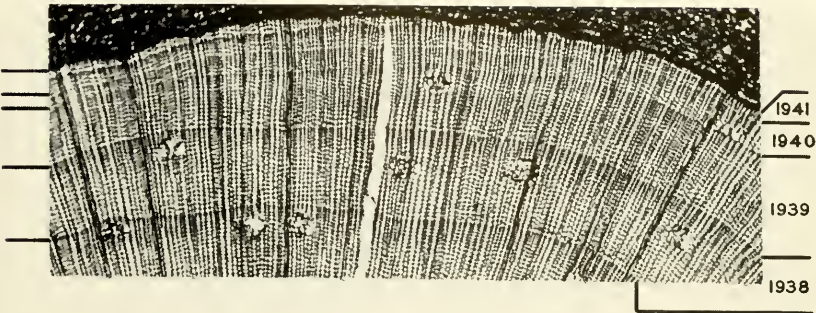


FIG. 1.

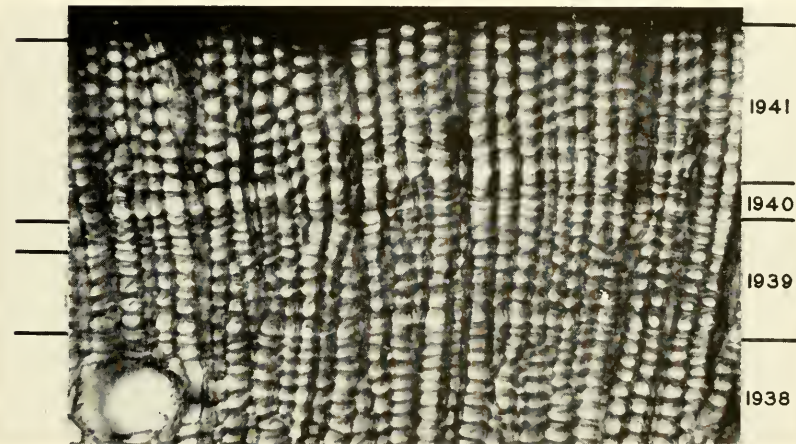


FIG. 2.

PLATE 18

- Fig. 1. *TTP 23-6-a*. Branch section of *Pinus ponderosa*, cut November 11, 1944.
Xylem of 1943-1944. Incipient intraseasonal growth fluctuation; transition between idw and ilw.
1943: Normal sce, with suggestion of growth fluctuation.
1944: idw or ilw as incipient multiplicity.
- Fig. 2. *TTP 24-2-a*. Branch section of *Pinus ponderosa*, cut November 29, 1941.
Xylem of 1937-1941. Separation and accentuation of the "double," or intra-annual gl, of 1940 contrasted with that of 1938; irregular margin under cambium.
1937: sce.
1938: Frost effects; tendency toward wide ddw.
1939: sce.
1940: Frost spots; s to d gl; sce.
1941: dce and an entire band of added growth (psg) with very irregular margin, reentrants filled with nucleated cells.

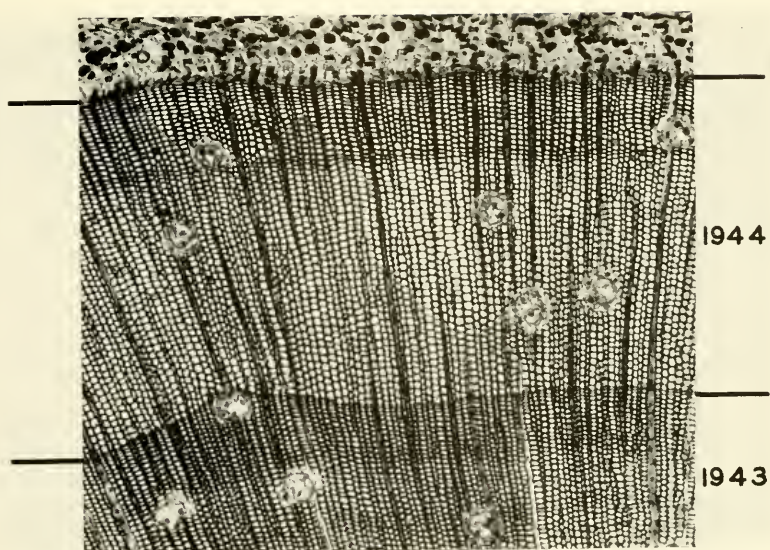


FIG. 1.

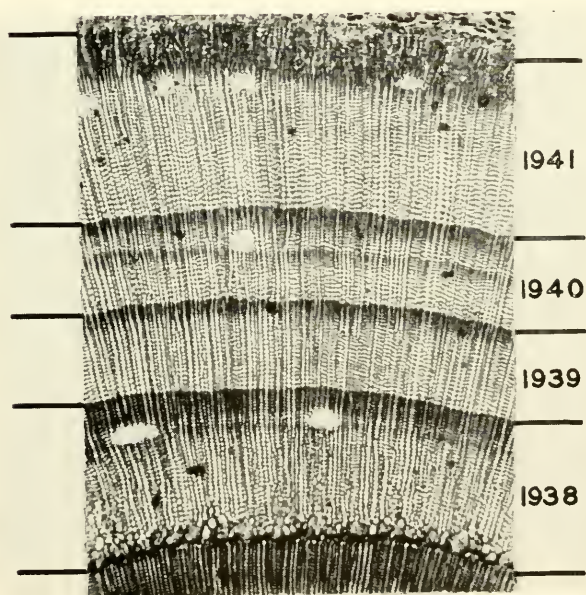


FIG. 2.

PLATE 19

Fig. 1. *TTP 24-3-b*. Branch section of *Pinus ponderosa*, cut November 29, 1941.

Xylem of 1937-1941. Atypical gls; dated multiplicity; irregular margin.

1937: 2 sce, each a typical gl.

1938: Zones of natural frost effects; sce partially indefinite.

1939: gl nearly all dw; msce; at places appears to be merely ddw of 1938.

1940: msce.

1941: Thin sce, in places dw only (appears to be ddw of 1940); inc. gl with irregular margin. Growth probably arrested on May 25, 1941, by artificial freezing.

Compare with plate 17, figures 1 and 2.

Fig. 2. *TTP 24-14-a*. Branch section of *Pinus ponderosa*, cut January 1, 1943.

Xylem of 1937-1942. Typical 1938 frost injury and recovery in a pine; masking of sharp intra-annual by absence of lw; diffuse dw as initial departure from unity.

1937: Diffuse dw bands; sce.

1938: Complete circle of natural frost effects; sce.

1939: sce.

1940: sce as example of initial departure from unity; sce with heavy band of dw which, by insertion of lw near an injury, proves to be 2 sce's.

1941: sce, with dw of variable width.

1942: sce.

In 1940 increment, outer dw of the annual lies against dw of the intra-annual except near an apparent injury where lw is inserted and 2 sce's are thus revealed. Separation of the 2 sce's can be followed under high power. See figure 3, below.

Fig. 3. *TTP 24-14-a*. Enlarged detail of figure 2, above. Xylem of 1940-1941.

Apparent idw in center of dw band is actually at contact between 2 entire gls, outer one here reduced to dw only; elsewhere on circuit, near an apparent injury, lw is inserted and sharp character of 2 gls is revealed. See figure 2, above.

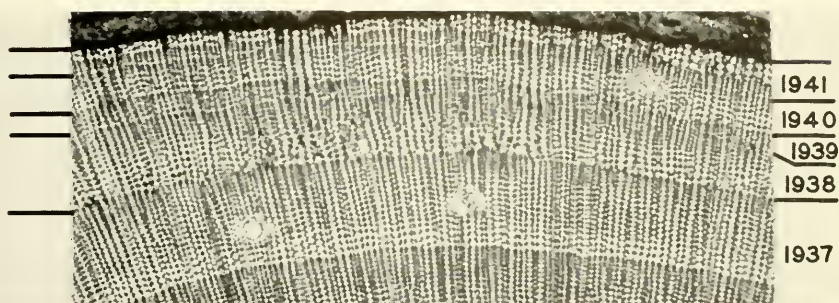


FIG. 1.

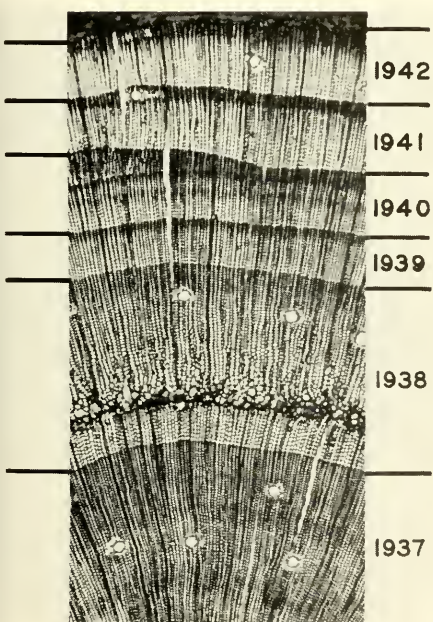


FIG. 2.

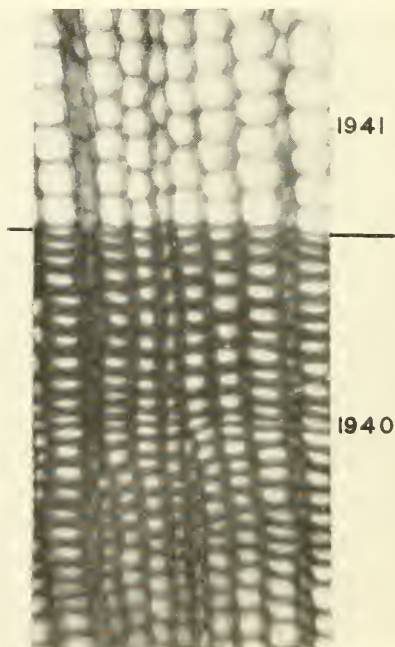
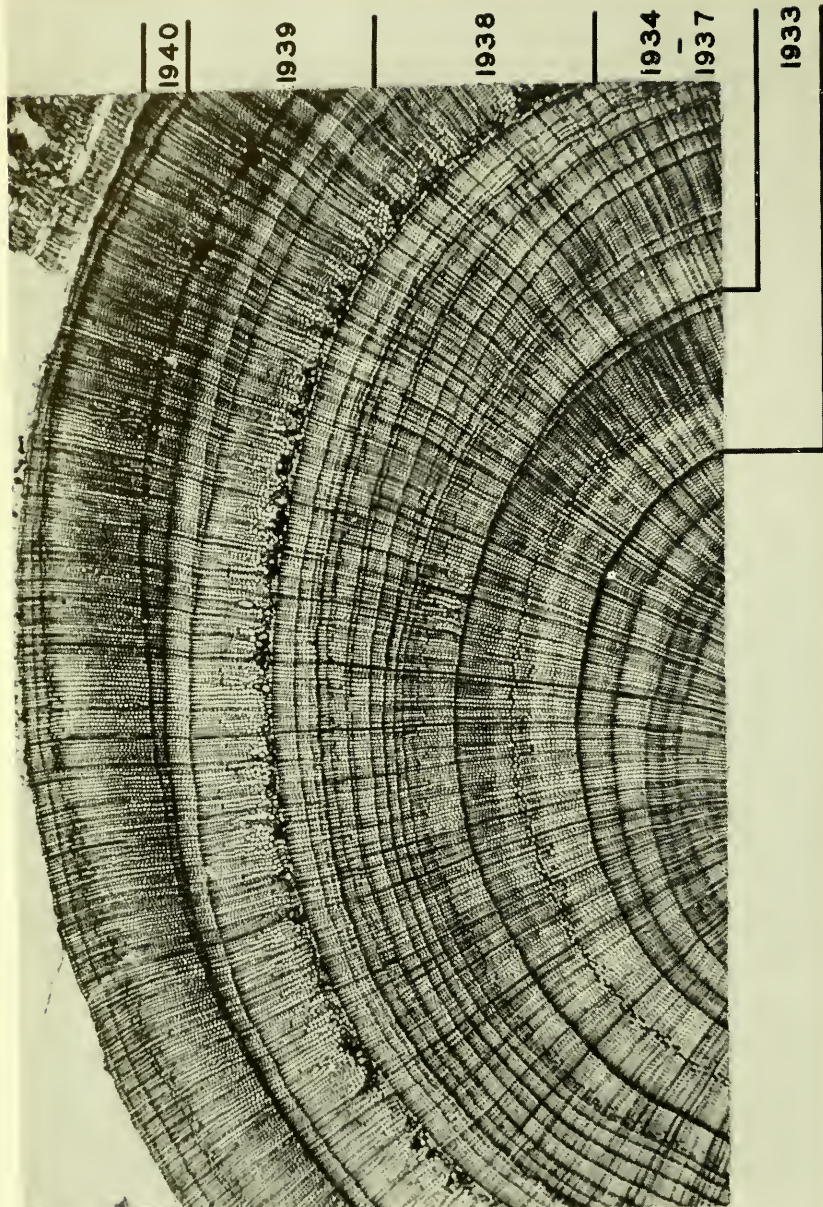
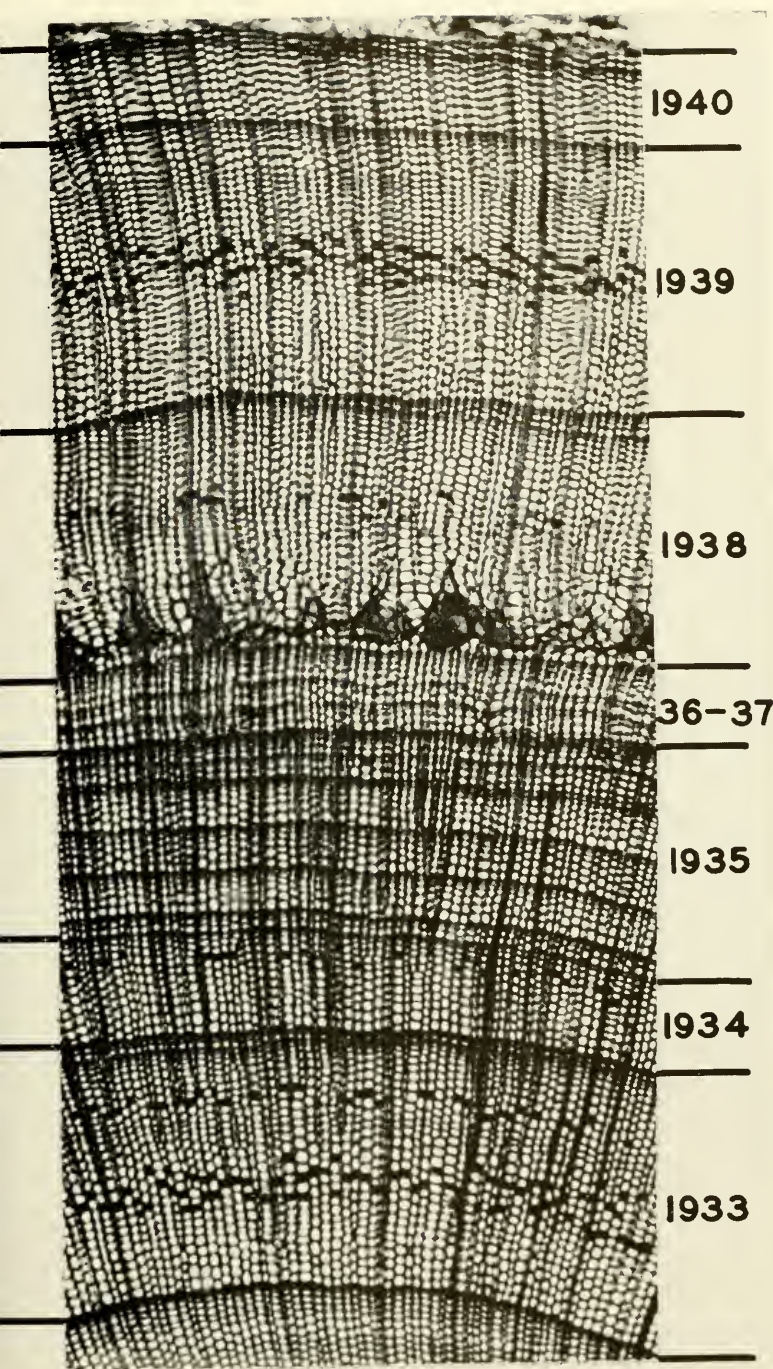


FIG. 3.



NSC 1-1-a. Branch section of *Cupressus arizonica*, cut May 10, 1940. Xylem of 1932-1940. Extreme multiplicity frost dated; typical frost effects; thin dw stringers; lensing and partial gels; frost-connected dw; parenchyma cells; growth to a certain date. 1932: annual dw; psec; see. 1933: see; sl. 1934: Spots of frost effects. 1934-37: Extreme multiplicity; lensing; dw stringers; annual dw; psec; see. 1938: Circle of frost effects; see; sl. 1939: Interior compound lens dated by spots of frost injury connected contacts uncertain. 1938: Circle of frost effects; see; sl. 1939: Interior compound lens dated by spots of frost injury connected contacts uncertain. 1938: Circle of frost effects; see; sl. 1939: Interior compound lens dated by spots of frost injury connected contacts uncertain.



NSC 1-1-a. Somewhat enlarged view from same section as plate 20. Xylem of 1932-1940. Extreme multiplicity in dated annual increments; lensing; dw stringers; ddw; annual margins indistinguishable from intra-annual; growth to a certain date. 1932: see with thickening dw. 1933: see with ddw which thickens tangentially by insertion of lw cells. 1934: 1-2 see, with dw of possible inner gl 1-cell thick. 1935: 5-6 see (at this position), two with weak dw. 1936-37: Possibly frost injury faintly shown; 3 gls with weak dw stringers. 1938: Typical frost injury and recovery; see; sl. 1939: Parenchyma circle; dcc; see (sharp here). 1940: see with ddw, amount of growth on May 10. Artificial freezing applied April 8, 1940.

PLATE 22

Fig. 1. *XSC 1-2-a*. Branch section of *Cupressus arizonica*, cut May 10, 1940. Xylem of 1935-1940. Dated multiplicity; eccentricity, with shifting long axis; lensing.

1935: Multiple.

1936: Natural frost effects; $\frac{1}{2}$ L's and rhythmic dw; see with weak, thin dw.

1937: Natural frost effects; see with weak thin dw; overlapping lenses with $\frac{1}{2}$ L's and rhythmic dw; see.

1938: Circle of natural frost effects; bands of dw; dce; see.

1939: see; interior lens and frost spots connected with dw; overlapping lens with $\frac{1}{2}$ L's and rhythmic dw; see.

1940: Effects of artificial frost (of April 8, 1940); sL.

Fig. 2. *XSC 2-1-a*. Branch section of *Cupressus arizonica*, cut May 10, 1940.

Xylem of 1933-1940. Dated multiplicity, 9 see for 4 years.

1933: see.

1934: Circle of natural frost effects.

1934-37: 9 see.

1938: Circle of natural frost effects; see.

1939: see; sL.

1940: Spots made by artificial frost of April 8.

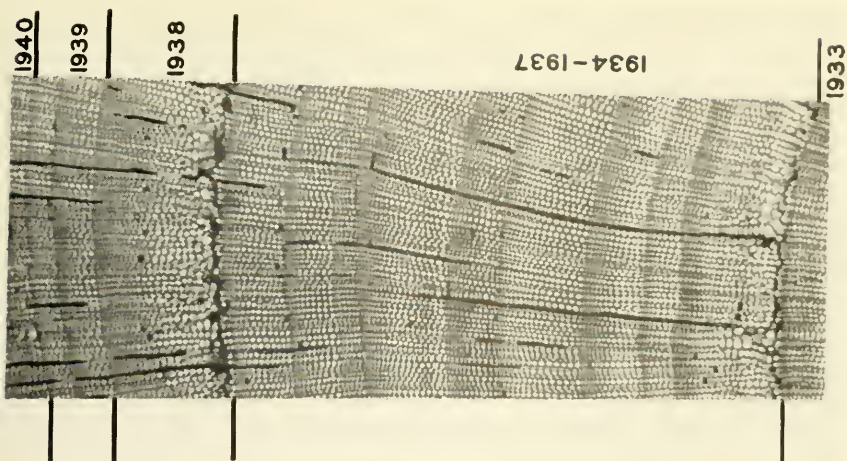


FIG. 2.

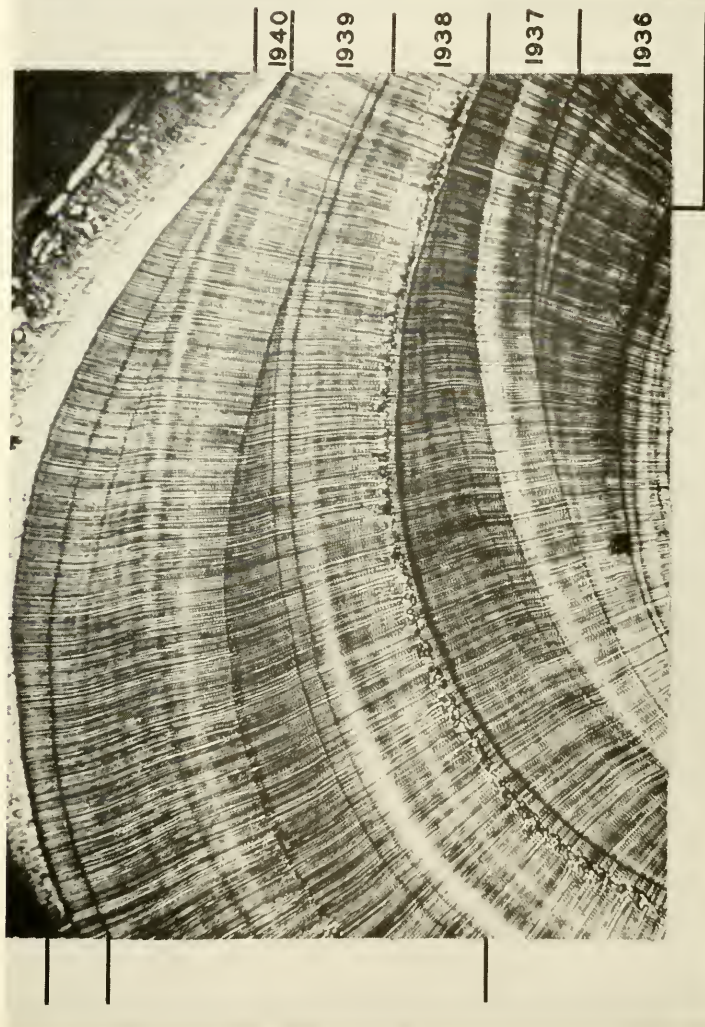


FIG. 1.

PLATE 23

Fig. 1. *XSC 2-2-a*. Branch section of *Cupressus arizonica*, cut May 26, 1940. Portion of 1936 annual increment. Dw so distributed as to give appearance of reversed sequence, lightest wood in the center.

Sequence as follows:

- (1) 2 cells of dw, with sharp contact that is masked by
- (2) dw, so close radially to dw of (1) as to give (1) a diffuse appearance; dw of (2) grades outward to
- (3) lw.
- (4) dw with sharp outer contact.

Lw grading both inward and outward into dw appears to give a reversed sequence. Features change tangentially; growing conditions induced different responses on different radii.

Fig. 2. *XSC 6-1-a*. Branch section of *Cupressus arizonica*, cut May 10, 1940. Xylem of 1937-1940. Dating by natural and artificial frost effects; multiplicity; ddw; initial and well-developed departures from unity of annual increment.

1937: 2 sharp gls, outer with ddw.

1938: Circle of natural frost effects; see with ddw, the inner band of ddw separating more widely and becoming diffuse.

1939: 2 see.

1940: Effects of artificial frost of April 8; inc.

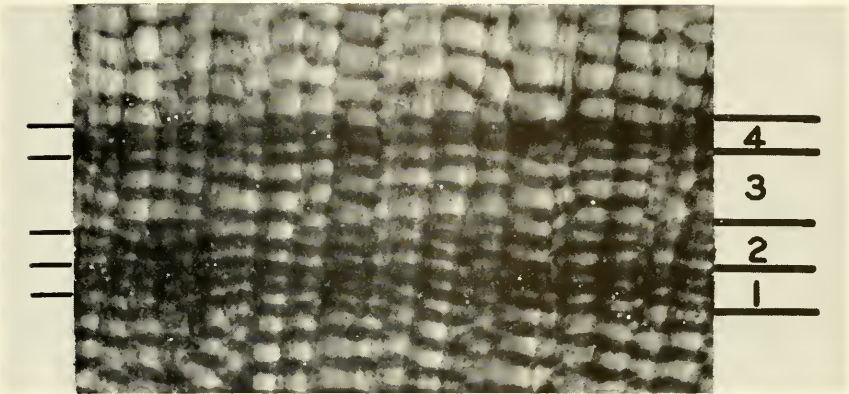


FIG. 1.

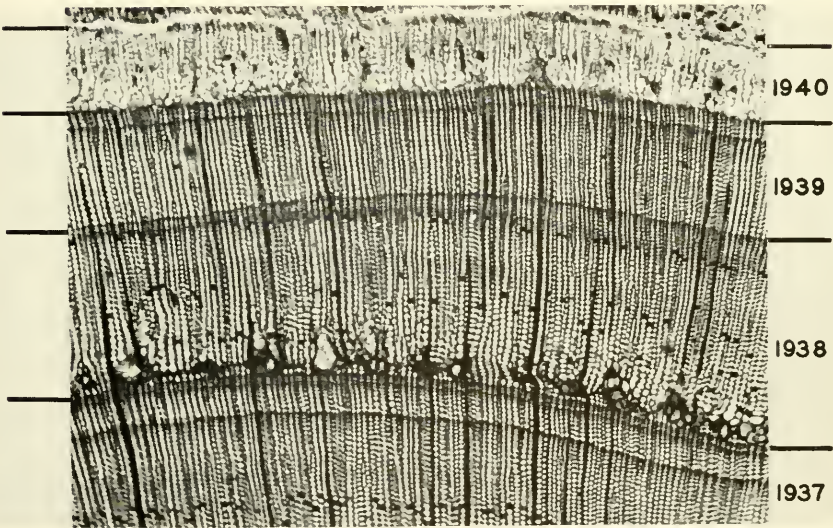


FIG. 2.

PLATE 24

Fig. 1. *XSC 6-1-b*. Branch section of *Cupressus arizonica*, cut May 10, 1940. Xylem of 1937-1940. Dating by natural and artificial frost effects; multiplicity; rhythms; lensing.

1937: Bands of dw; $\frac{1}{2}$ L's; sce.

1938: Circle of natural frost effects; bands of dw; sce; sL.

1939: Spots by natural frost; bands of dw; $\frac{1}{2}$ L; sce; sL.

1940: Effects of artificial frost of April 8; inc.

Without the presence of absolute dating criteria, the possibility of error in dating gls is obvious.

Fig. 2. *XSC 8-3-b*. Branch section of *Cupressus arizonica*, cut May 11, 1941. Xylem of 1938-1941. Multiplicity; "outer thin" intra-annual; "added-on" lens of 1940; artificial frost injury; growth to a certain date.

1938: dce and sce, resembling widely spaced ddw.

1939: Slight curtain effect; natural frost spots; parenchyma circle; sce; sL which began as ddw and grades into a curtain in other direction; "outer thin" sce.

1940: Curtain effect; parenchyma circle; psce; sce whose dw separates by insertion of lw, outer contact weakened; "added-on" sL.

1941: inc. e gl; most recent cambial derivatives and initials disrupted by artificial frost of May 9. Wettest April and May on record.

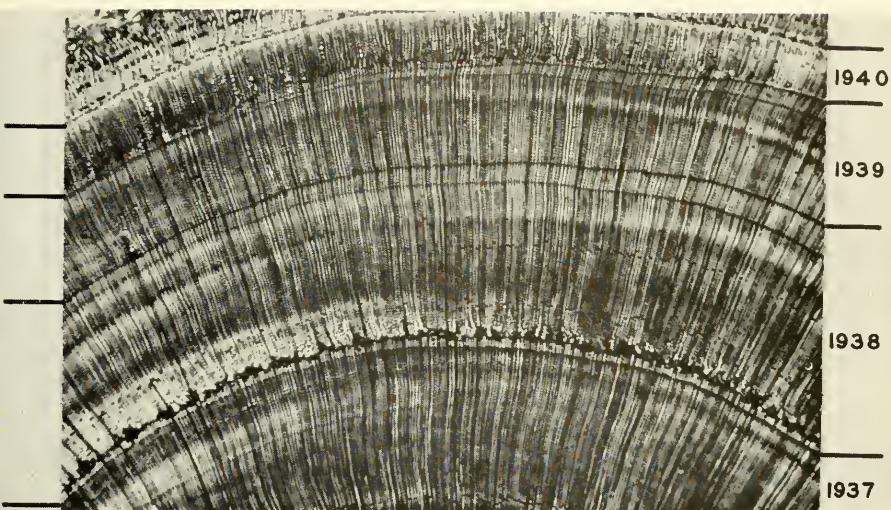


FIG. 1.

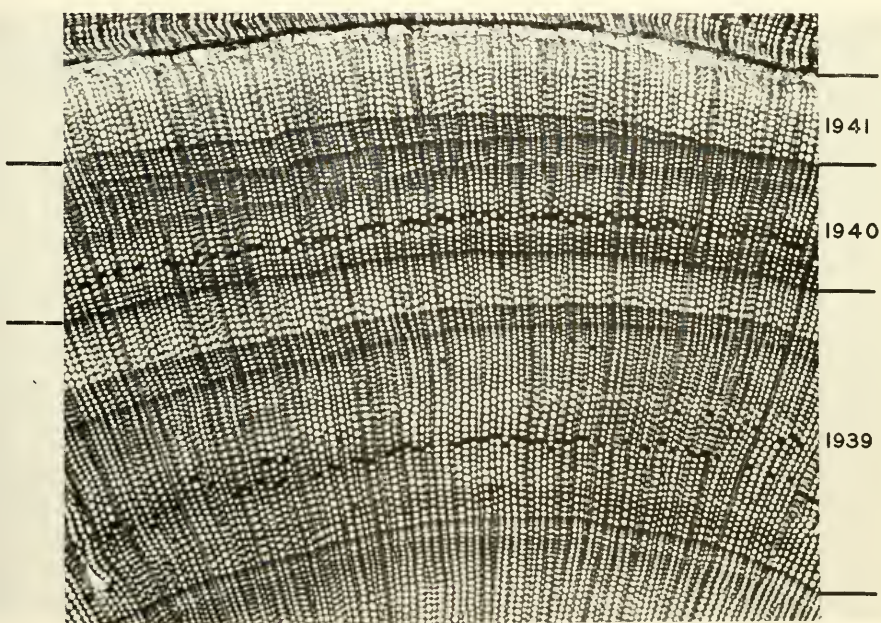
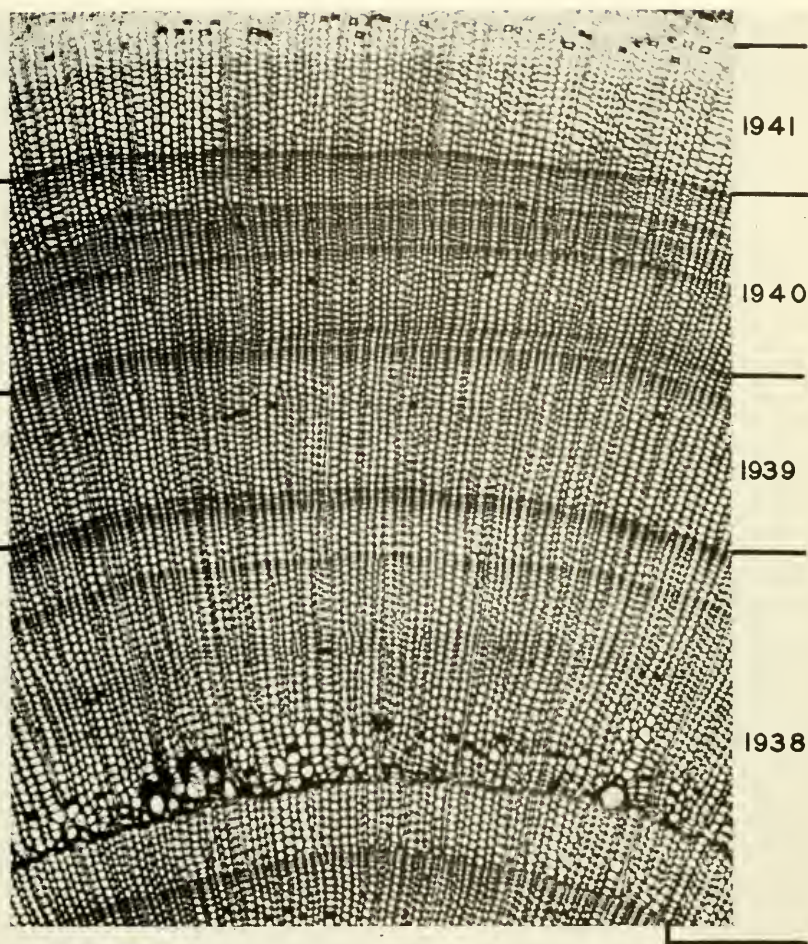


FIG. 2.

PLATE 25

- XSC 8-4-a. Branch section of *Cupressus arizonica*, cut May 13, 1941. Xylem of 1937-1941. Multiplicity and growth layer contacts—weak annuals and also weak intra-annuals; "outer thin" gl with faint indefinite dw; ddw.
- 1937: see, masked partially by slight frost injury at start of 1938.
- 1938: Incipient inner natural frost; effects of natural frost with dw cells; faint dee; see; see with strong dw and ddw.
- 1939: see with strong outer dw over part of circuit and very weak dw over a lens. Note contrast of outer margins over various parts of circuit. The lens definitely a second cycle of cambial activity.
- 1940: msce; s arc; 2 see (contacts of intra-annuals become less sharp outward on branch).
- 1941: inc. e gl, to May 13. Branch frozen May 9, 1941, 13.5 cm. outward from this section.
- (Low magnifications on unstained sections without criteria of absolute dating would encounter difficulty in distinguishing all annual from all intra-annual contacts.)





XSC 9-1-a. Branch section of *Cupressus arizonica*, cut May 23, 1941. Xylem of 1938-1941. Longitudinal variation of intra-annual contacts, plates 26, 27, and 28, figure 1; growth rhythms.
1938: sce at center.
1939: Multiple diffuse dw's; msce.
1940: Multiple diffuse dw's; msce which changes to psce 15 cm. outward and to dce 25 cm. outward on the branch; sce.
1941: inc.



XSC 9-1-b. Section taken 15 cm. outward on branch section shown on plate 26.

Xylem of 1939-1941. Intra-annual psce of 1940 is msce 15 cm. inward (pl. 26) and dee 10 cm. outward on branch (pl. 28, fig. 1); growth rhythms.

1939: dee; msce. Cell columns bent both clockwise and counterclockwise.

1940: Curtainlike dw; multiple bands of diffuse to definite dw; psce which is msce on plate 26; mostly dee but partly sharp dw near outer part of increment (faint in pl. 26); msce; sL which is present as expanded dw in plate 26.

1941: inc. Frozen artificially May 9, 1951.

In passing outward from sections *a* to *b*, the axis of the diffuse margin has rotated clockwise and the axis of the outer lens of 1940 has rotated counterclockwise.

PLATE 28

Fig. 1. *XSC 9-1-c*. Section 10 cm. outward on branch from plate 27. Xylem of 1939-1941. Intra-annual dce of 1940 which is psce 10 cm. inward and msce 25 cm. inward on branch; sharpening of contacts inward on branch; growth rhythms.

1939: sce with indefinite margin; cell columns doubly bent.

1940: Multiple bands of dw; dce which is psce on plate 27 (partially or wholly diffuse intra-annual of 1940 unusual in other branches of this tree and in other trees); dL rather faint—may be the sL on plate 27; sce.

1941: dce and parenchyma circle; inc.

Fig. 2. *XSC 10-5-a*. Branch section of *Cupressus arizonica*, cut May 9, 1941. Xylem of 1938-1941. Dated multiplicity; contrast of "outer thin" gls of 1939 and 1940; growth to May 9.

1938: sce with irregular margin.

1939: Possible frost injury; parenchyma circle with dw; bands of diffuse dw; 2 sce, outer (annual) dw the heavier.

1940: dce; bands of diffuse dw; sce, with ddw; "outer thin" sce actually long lens because of a branch. Inner dw (intra-annual) heavier than the outer (annual).

1941: inc.



FIG. 1.



FIG. 2.

PLATE 29

XSC 11-1-a. Branch section of *Cupressus arizonica*, cut August 20, 1941. Xylem of 1937-1941. Variable definition of outer contact of annual increment; dw of "outer thin" gl sharp to nearly nonexistent; multiplicity; typical 1938 natural frost effects.

1937: Diffuse bands of dw; dL; sce.

1938: Effects of natural frost (see pl. 30, fig. 1); dce; psL; sce.

1939: Inner gl, fairly s border, clockwise its dw breaks twice in succession and lifts away in dL's; "outer thin" gl, its dw changing from thin and sharp to very faint and diffuse. Without typical frosts of 1938, 1939, and 1940 (last two present elsewhere on section) to date the gls, the "outer thin" of 1939 could scarcely be identified as annual; if it were, then 1939 annual increment would include 2 gls.

1940: Thin sce.

1941: Nearly complete; scattered cells of psg. Artificial freezing outward on branch.

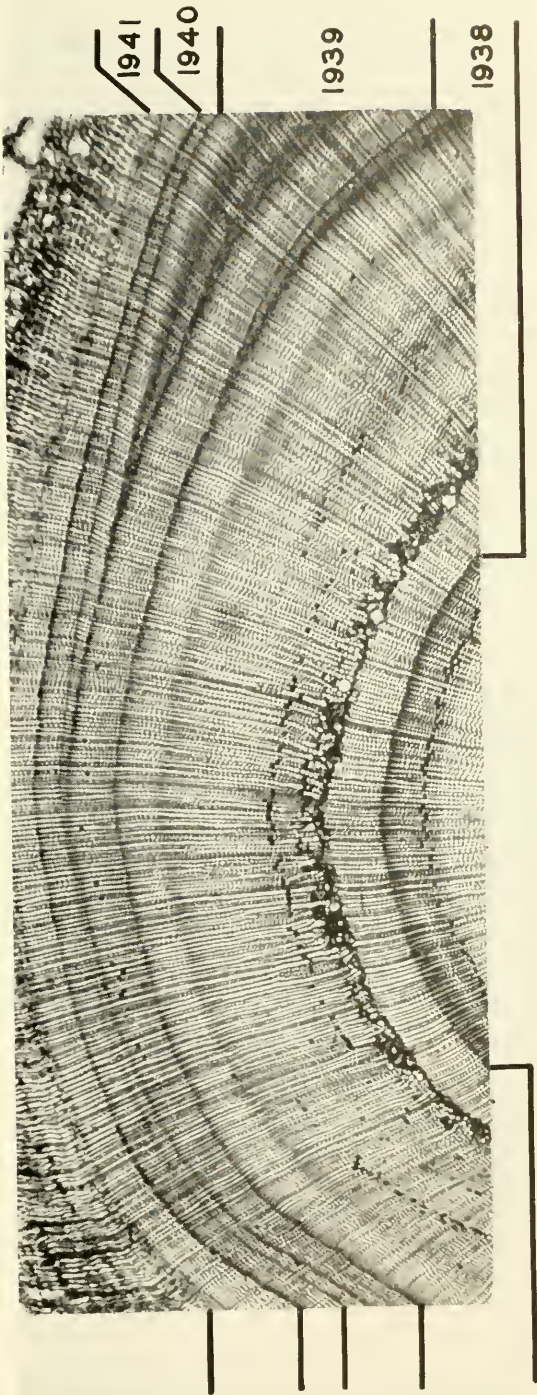


PLATE 30

Fig. 1. *XSC 11-1-c*. Branch section of *Cupressus arizonica*, 9 cm. outward on branch from plate 29, cut August 20, 1941. Xylem of 1937-1941. Definite gl made by natural frost; weak annual contact of 1939 and "outer thin" gl.

1937: sce with ddw.

1938: Definite gl, an extension around circuit of frost injury; dce; sce with thin dw.

1939: sce with heavy dw which separates into two indefinite bands; "outer thin" gl with dw 1 cell thick.

1940: sce with irregular outer contact.

1941: inc; cambium dead by artificial freezing of May 9, 1941.

Fig. 2. *XSC 11-2-a*. Branch section of *Cupressus arizonica*, cut September 11, 1941. Xylem of 1937-1941. Contrast of weak "outer thin" gl of 1939 and strong outer gl of 1940; contrast in 1939 of strong intra-annual dw and weak annual dw; different sequences on different radii; psg.

1937: psce.

1938: Natural frost effects with parenchyma and dw cells; bands of diffuse dw; dL; sce.

1939: Frost spots; bands of diffuse dw; sce with fairly heavy dw which separates into two indefinite bands; "outer thin" gl with thin, weak, intermittent dw. Actually, both sce's are diffuse over a portion of their contacts.

1940: msce; sce; sL.

1941: sce; psg; cambium probably dead, as an effect of artificial freezing outward on branch May 9.

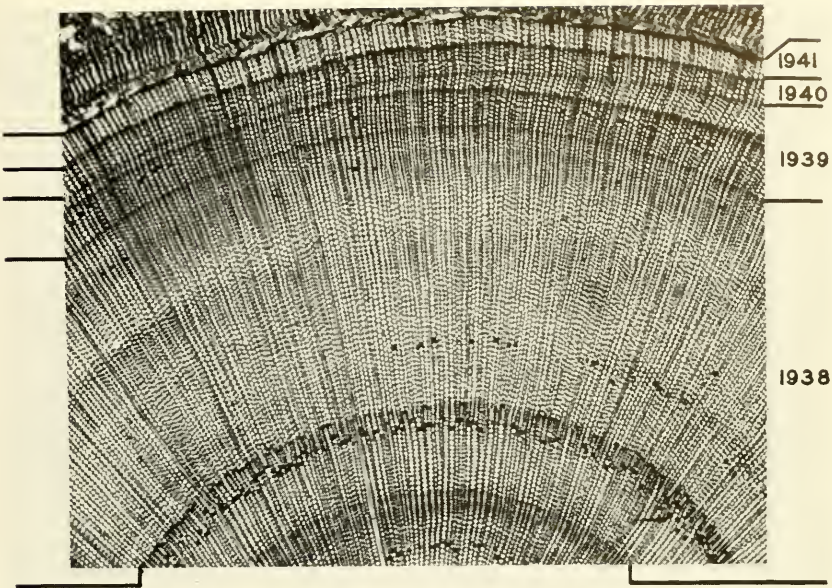


FIG. 1.

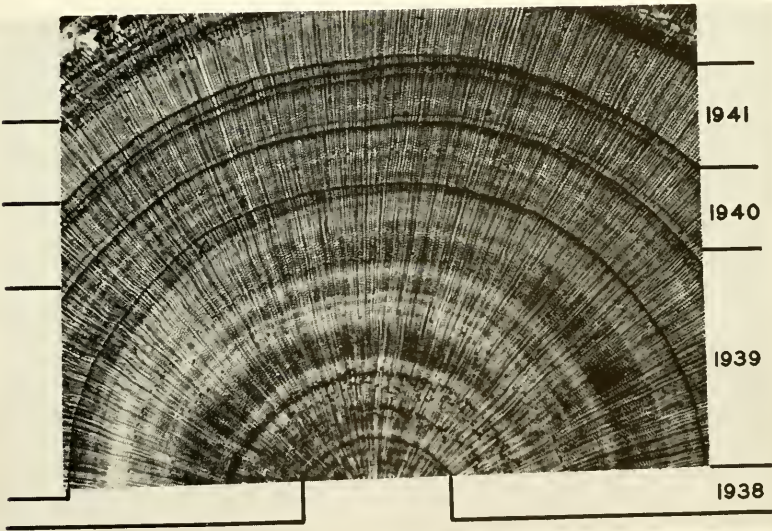


FIG. 2.

PLATE 31

Fig. 1. *NSC 11-3-b*. Branch section of *Cupressus arizonica*, cut September 27, 1941. Xylem of 1938-1941. Striking "outer thin" gl of 1939 and evidence of its age by position of 1940 frost effects; weak and thin dw of "outer thin" gl of 1939 contrasted with stronger dw of outer 1939 on figure 2, below; ddw changing to a ce gl; multiplicity.

1938: see with wide ddw.

1939: see with strong dw; "outer thin" see with weak dw.

1940: Effects of natural frost; see with ddw becoming separate gl.

1941: inc; cambium probably dead, killed by artificial freezing of May 9, 1941.

Fig. 2. *NSC 11-3-c*. Branch section 6 cm. outward from that of figure 1, above. Xylem of 1938-1941. In contrast with figure 1, dw of "outer thin" gl of 1939 is much stronger; multiplicity.

1938: see with weak dw.

1939: Inner gl with sharp dw which separates into 3 diffuse bands; "outer thin" gl here much wider and possessed of stronger dw than elsewhere in this branch and in other branches.

1940: see with heavy dw and irregular outer contact.

1941: inc; cambium dead, killed by artificial freezing of May 9, 1941.

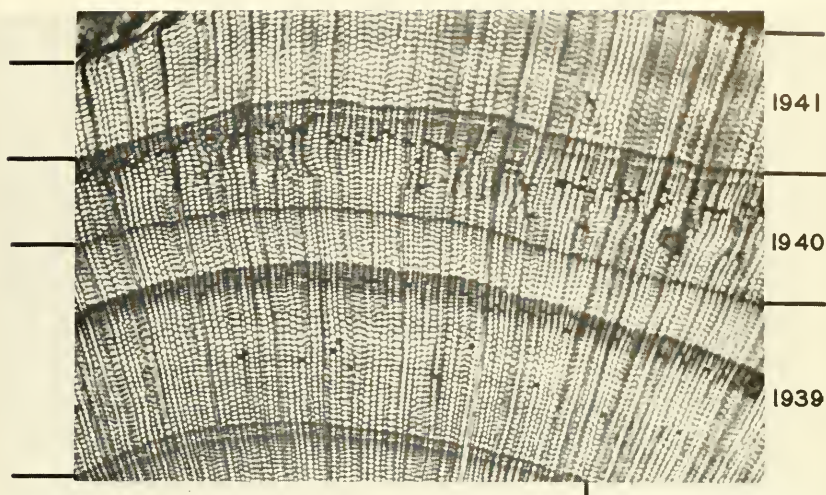


FIG. 1.

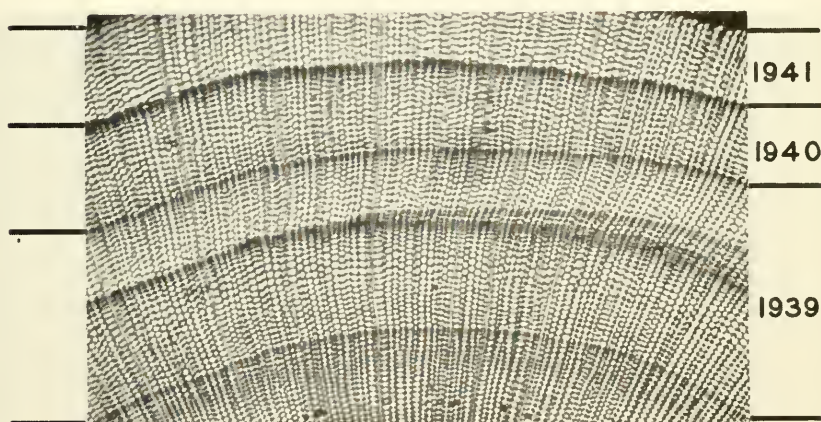
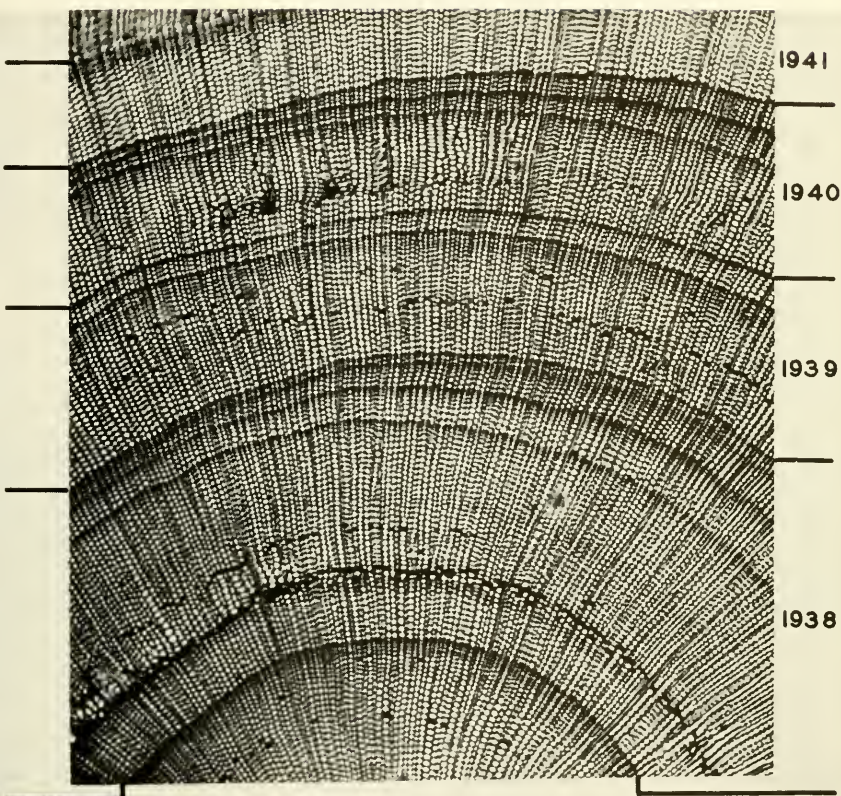
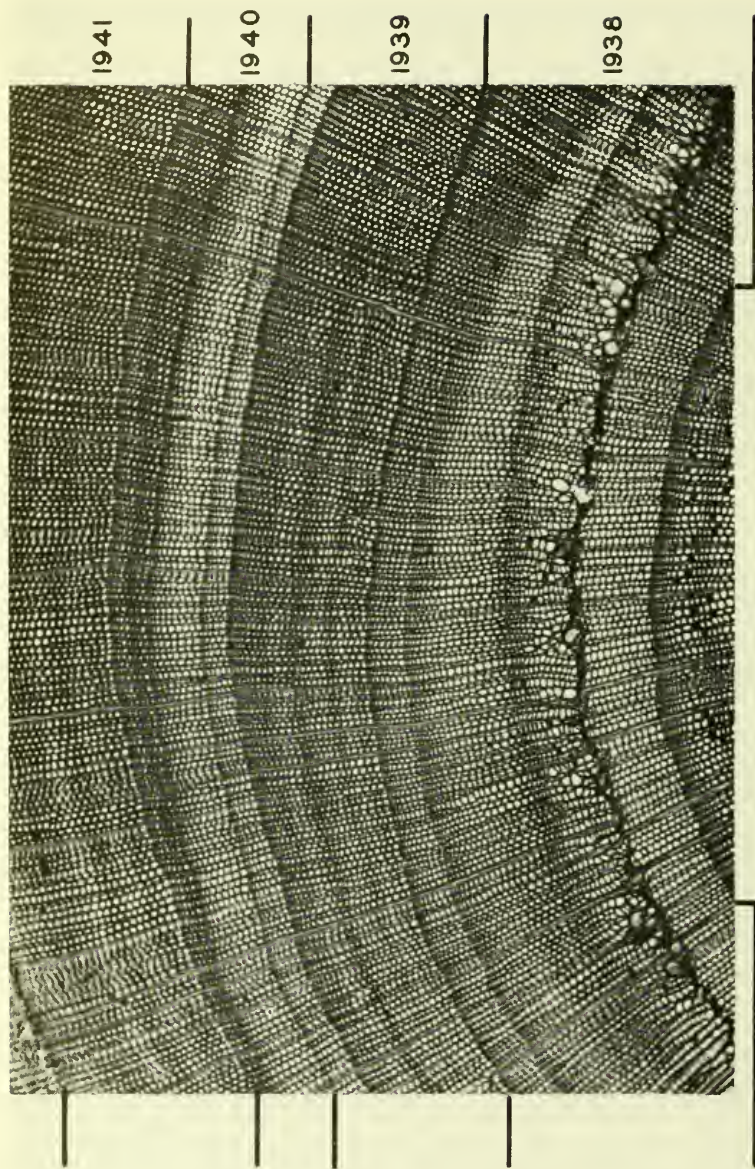


FIG. 2.

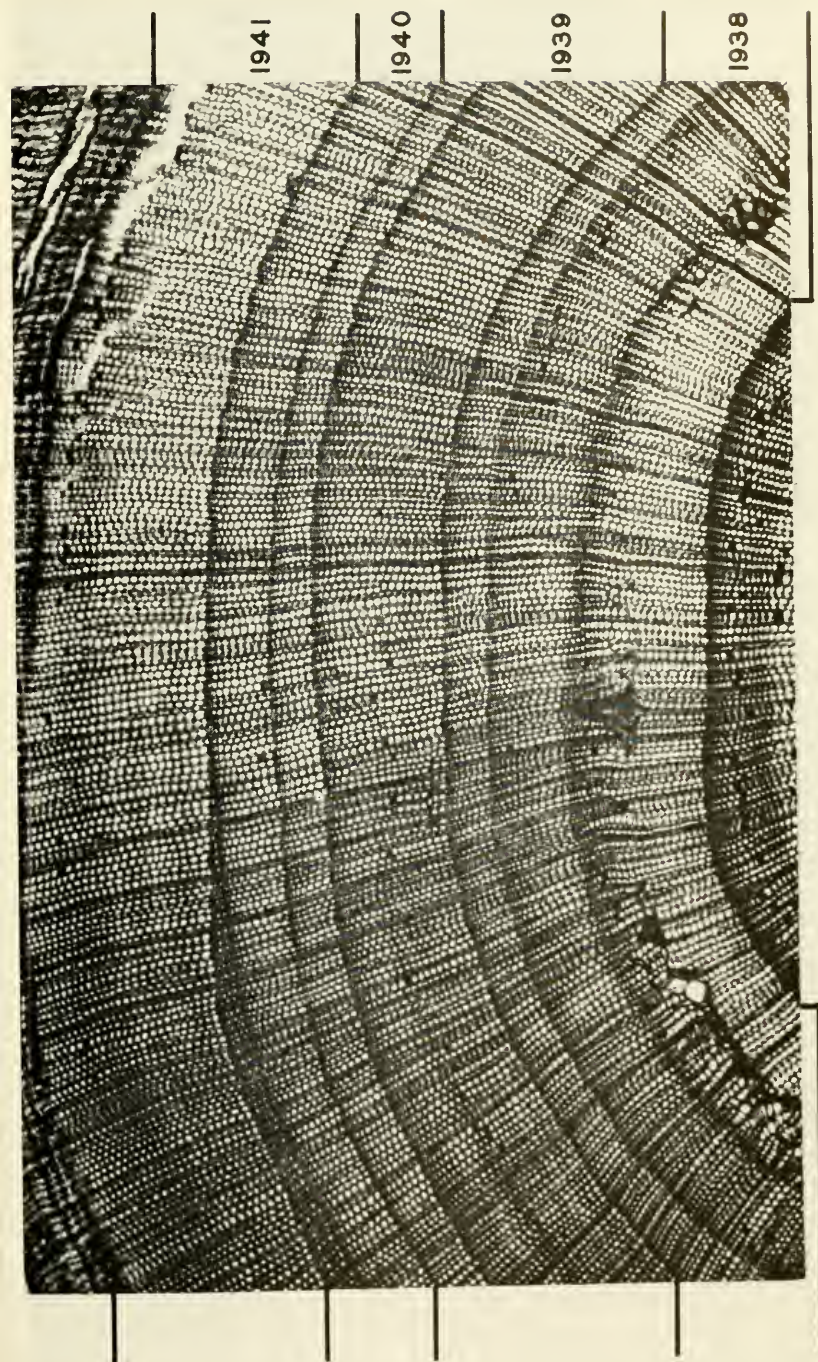
PLATE 32

XSC 12-1-a. Branch section of *Cupressus arizonica*, cut October 11, 1941. Xylem of 1937-1941. Typical pattern of thin and thick gls giving a "fingerprint"; dated multiplicity; ddw; psg. Frost effects with parenchyma and dw cells, 1938; frost spots, 1939; frost spots, 1940. The "fingerprint"—
1937: A thick sce.
1938: A thick sce.
2 very thin sce (plus ddw).
1939: A thick sce.
A very thin sce.
1940: A thick sce.
2 very thin sce.
1941: A thick sce; cells of psg.
This pattern includes both intra-annual and annual gls.





XSC 13-2-a. Branch section of *Cupressus arizonica*, cut June 27, 1941. Xylem of 1937-1941. Complementary status of sharp arc margins and variations in identity of sharp contacts on different radii: "outer thin" gl of 1939; typical frost effects of 1938; multiplicity; lensing; growth rhythms, 1937; dec; see, 1938: Typical frost effects; 2 arcs which diffuse in opposite directions, i.e., each sharp radially where the other is diffuse; see, 1939: Rhythmic dw;



(See legend on following page.)

PLATE 34

- XSC 13-2-b. Branch section 4.5 cm. outward from plate 33. Xylem of 1937-1941. Longitudinal variation; dw with frost effects; stringers of dw; "outer thin" gl; multiplicity.
- 1937: dce; sce.
- 1938: Frost effects and accompanying dw; 2 sce, with dw of about equal weight.
- 1939: 2 sce, dw of "outer thin" slightly weaker than inner (compare with pl. 33).
- 1940: sce whose dw expands into "stringers."
- 1941: Partly inc.

PLATE 35

- Fig. 1. XSJf 1-1-a. Branch section of *Pinus jeffreyi*, cut June 12, 1940. Xylem of 1937-1940. "Outer thin" gl and dated multiplicity in a pine; two stages of departure from unity: diffuse and sharp intra-annuals; midincrement curtain (or reversed sequence).
- 1937: Faint dce; sce with irregular contact.
- 1938: Effects of natural frost; 2 dce resembling reversed sequence with lw in center; sce.
- 1939: 2 sce, inner dw stronger than that of the "outer thin" gl (outer thin becomes weaker outward on branch).
- 1940: inc. (Branch frozen artificially 15 cm. outward on branch, May 10.)
- Fig. 2. XSP 1-2-a. Branch section of *Pinus ponderosa*, cut February 22, 1941. Xylem of 1937-1940. Multiplicity in a pine; variation in contact definition.
- 1937: Faint dce; sce.
- 1938: Slight frost effects; sce with ddw.
- 1939: dce; sce.
- 1940: sce with strong, sharply bordered dw; gl with weak, indefinite, at places nearly invisible dw but resembles outer (or annual) margin of 1939 in plates 33, 30, 29; gl (under cambium) with poorly developed or absent dw.

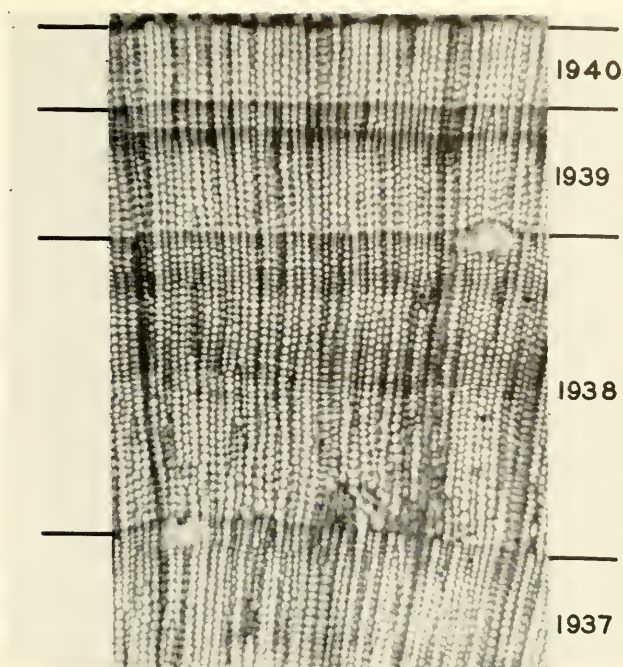


FIG. 1.

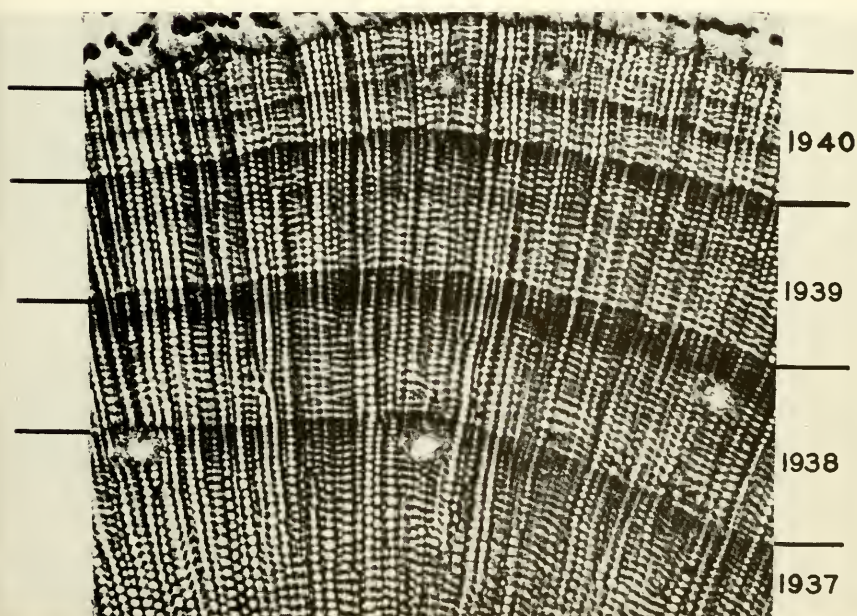


FIG. 2.

PLATE 36

- Fig. 1. *YCt 2-1-b*. Branch section of *Citrus maxima*, cut November 26, 1940. Portion of xylem for 1939-1940. Extreme multiplicity in an irrigated dicot grown at Yuma, Ariz. Twelve or more gls for 1 to 2 years.
- Fig. 2. *YCt 2-5-a*. Branch section of *Citrus maxima*, cut November 26, 1940. Xylem of 1939-1940. Multiplicity in a dicot; complex lensing; probable effect of irrigation. Six to twelve gls for 4 tip flushes for 2 years.

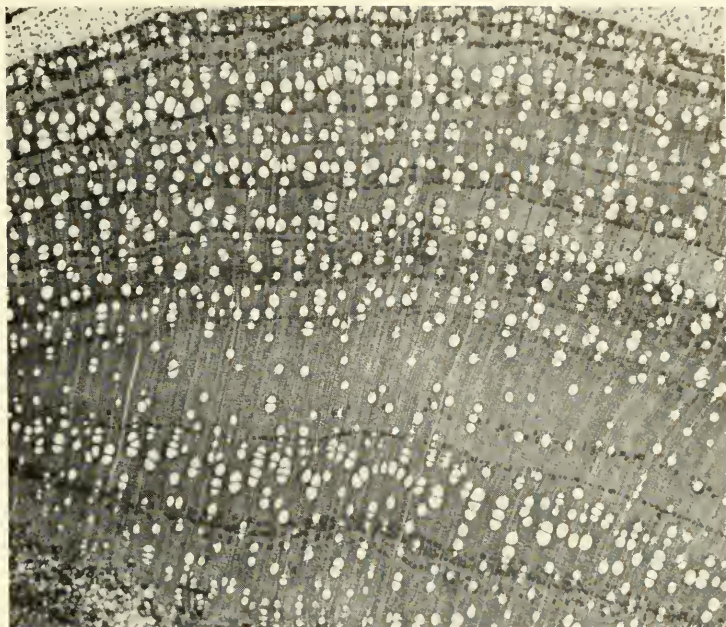


FIG. 1.

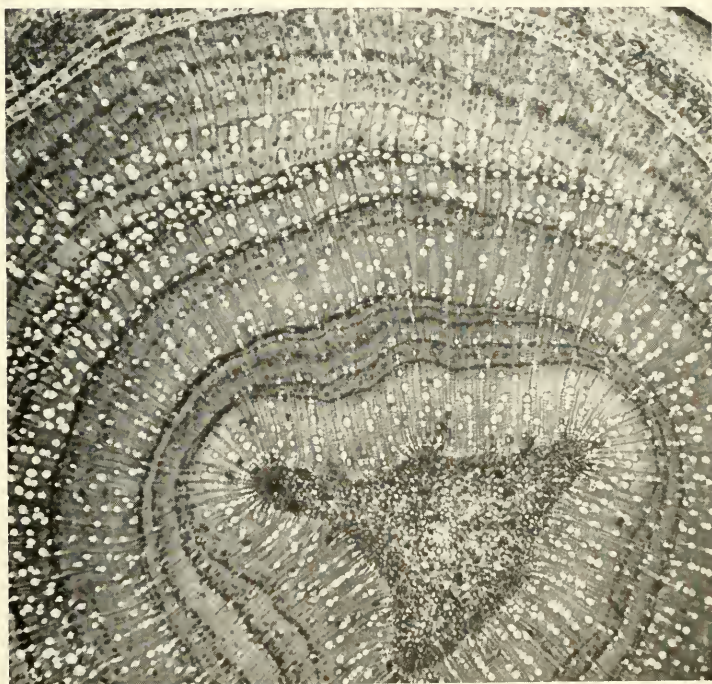


FIG. 2.

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SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 140, NO. 2

Charles D. and Mary Vaux Walcott
Research Fund

PLEISTOCENE BIRDS IN BERMUDA


(WITH THREE PLATES)

By
ALEXANDER WETMORE
Research Associate
Smithsonian Institution



(PUBLICATION 4423)

CITY OF WASHINGTON
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PLEISTOCENE BIRDS IN BERMUDA

BY ALEXANDER WETMORE

Research Associate, Smithsonian Institution

(WITH THREE PLATES)

In July 1956, Dr. David Nicol, then Associate Curator of Invertebrate Paleontology and Paleobotany in the U. S. National Museum, visited Bermuda to collect mollusks and other material, traveling under funds supplied by the National Science Foundation and the Walcott Fund of the Smithsonian Institution. On July 21 he worked in a Quaternary fossil deposit in the H. Bernard Wilkinson Quarry, south and west of Coney Island, Hamilton Parish, Bermuda. At this site, which is one that had been located by Dr. Heinz Lowenstam of the California Institute of Technology during his studies of the geology of the islands, in addition to fossil mollusks Dr. Nicol collected 30 fragments of bones of birds. Among these there were parts of a crane-like bird, unlike any living species, and wholly unexpected from this island locality.

In view of the importance of this discovery, Dr. W. H. Sutcliffe, Jr., Director of the Bermuda Biological Station, kindly arranged to have a further collection made for me in the cave where the first specimens had been obtained. Subsequently, in 1958, agreement was made with David B. Wingate to make a search for further avian material.

The bones, with quantities of shells of land mollusks, were imbedded in a calcareous tufa, fairly soft in texture, so that they were cleaned without particular difficulty. Their preservation is unusual as, in many, lines of muscle attachment and the most delicate processes are intact. Some of the specimens, in fact, are as perfect as the corresponding parts in the modern skeletons with which they have been compared.

The actual age of such deposits on Bermuda may be established by the detailed geological studies that Dr. Lowenstam has had underway. It is certain that they are old, and for the present it is my assumption

that they date back to the Pleistocene. The land area available at Bermuda during the lowest sea level of Pleistocene time was limited, as beyond the present shallow banks that surround the islands the bottom falls off steeply to a considerable depth.

Occurrence of the Bermuda petrel, the cahow of the early settlers, in Pleistocene time is not to be classed as unusual, but the crane and the duck present interesting records which indicate that the peculiarities of the avifaunas of the Pleistocene known in the West Indies (including the Bahama Islands) extended also to the remote Bermudas.

Drawings illustrating the specimens have been made by Lawrence B. Isham.

Family PROCELLARIIDAE, Shearwaters, Fulmars

PTERODROMA CAHOW (Nichols and Mowbray): Bermuda Petrel

Aestrelata cahow Nichols and Mowbray, Auk, vol. 33, No. 2, April (March 31), 1916, p. 194. (Southeast side of Castle Island, Bermuda.)

The numerous bones in the deposit indicate that the cahow was as abundant in this period of the Pleistocene as it was in the early days of colonists who settled on Bermuda. The material, which is rather fragmentary, includes representation of the humerus, ulna, carpo-metacarpus, furcula, coracoid, femur, tibiotarsus, and tarsometatarsus. These do not differ from modern specimens in the collections of the United States National Museum.

Family ANATIDAE, Swans, Geese, Ducks

ANAS PACHYSCELUS sp. nov.

(Pl. I, figs. 1-5)

Holotype.—Left tarsometatarsus, U.S.N.M. No. 22506, complete except for part of talon, from H. Bernard Wilkinson Quarry, south and west of Coney Island, Hamilton Parish, Bermuda.

Characters.—Tarsometatarsus similar in general form to that of modern *Anas bahamensis* Linnaeus; size decidedly larger, being equal in length to that of male *Anas platyrhynchos*, with the shaft more robust than in the nominate race of that species; central line of the two that mark the attachment of the tibialis anticus extended distally for half its length below the lower end of the outer line; posterior face of upper end of shaft with a shallow, well-marked sulcus extending past base of inner side of talon; trochleae relatively broader and heavier.

The collection contains four nearly entire tarsometatarsi in addition to the type, with four proximal and three distal ends of others.

Tibiotarsus.—Fragments of this element include parts of 9 anterior and 16 posterior ends. The more robust have the head, the shaft, and the condyles, particularly the outer one, somewhat heavier than in larger individuals of male *platyrhynchos*, though the fibular crest is shorter. The range in size is that normal in individual and sexual differences.

Femur.—This bone is represented by 6 that are nearly complete, with 12 other parts from either end. Four others, all but one complete, come from ducklings from two-thirds grown to nearly full size. The material shows the usual size variation found in ducks of the subfamily Anatinae. The fossil bones as a whole indicate heavier form, but slightly shorter length, in comparison with a similar series of *A. platyrhynchos*. The more robust size is evident in the proximal end, and at the center of the lower surface of the shaft which is more broadly rounded, less angular. The popliteal area appears broader.

Humerus.—Six nearly complete bones, and 20 fragments are referred to this species. In form these are quite uniform, with the differences in size those common between male and female. However, it is to be noted that the larger group, presumed to come from male individuals, have the dimensions of female *Anas platyrhynchos*, and are thus definitely smaller than that species. The head of the bone is reduced in size, and is less undercut on the anconal aspect, so that there is no overhang above the upper end of the shaft. The external outline of the deltoid crest is more rounded, less angular, and the external tuberosity, viewed from the upper side, is supported on a narrower base. The elevated line of the attachment of the latissimus dorsi anterioris is decidedly shortened, but at the same time is produced as a sharp ridge that is more prominent than in any of the modern species of ducks that I have seen. At the distal end the external condyle is reduced, and the brachial depression is shallower, with less definite outline.

The impression from these comparisons is that the bird was one of sedentary habit and weakened powers of flight compared to the strong-flying, living species with which it has been compared. In support of this supposition I find that the humerus of this fossil species of Bermuda, in those points in which differences have been described above, agrees rather closely with the same bone in living *Anas laysanensis* Rothschild, which lives around the lagoon on Laysan Island in the Hawaiian Wildlife Refuge, where it is completely sedentary.

Ulna.—The two nearly complete bones show the amount of difference in size common to male and female in living species in their group. There are 12 additional fragments. These show that the middle section of the wing is decidedly shortened, the larger of the two complete specimens being definitely less than in the female of *Anas platyrhynchos*. It is interesting also to observe that the two lines of papillae for feather attachment have slight development of the series on the anconal side, which are prominent in birds of strong flight.

The two fragments of the radius seen are too small to give useful points for comparison.

Carpometacarpus.—This is represented by 1 complete bone, 3 others with the main shaft of metacarpal III missing, and 12 additional fragments. The complete elements show the slight differences in size that are considered to be due to sex, since they correspond to this distinction in living Anatinae. Compared to *Anas platyrhynchos*, the longer fossil bones, presumed to be male, are equivalent in length to the female of the living bird. The reduction in length seems to have come in the shafts of metacarpals II and III, as the proximal and distal ends are equal in size to those of the living species. The fossil carpometacarpus has its principal peculiarity in a pronounced constriction of the anterior end of the shaft of metacarpal III, which at first glance is somewhat confusing as it suggests the form found in the diving ducks. The other contours of the entire bone however are those of species of the Anatinae.

The slight differences described are those to be anticipated in a species of reduced flight.

Coracoid.—Ten bones nearly complete and nine fragments illustrate the characters of this bone. The element as a whole is definitely weaker than in the living mallard, as the length is slightly shorter, and the entire bone is less robust. This is noted in the reduction in the brachial tuberosity, the smaller glenoid facet, and the shortened procoracoid, in the head, and in the narrower sternal facet at the opposite end. Only in the coraco-humeral surface is there no noticeable difference.

Scapula.—The proximal sections of eight scapulae serve to indicate slightly smaller size and relatively more slender shaft, compared to *Anas platyrhynchos*.

Miscellaneous.—Additional parts of the skeleton include five fragments of the synsacrum, which resemble the similar part in other Anatinae, and are slightly smaller than those of the mallard.

Basal phalanges of three anterior toes equal in size those of male *Anas platyrhynchos*, so that the foot was large.

Discussion.—In this examination of the available parts of the skeleton, comparisons have been made with the modern mallard, *Anas platyrhynchos* Linnaeus, as the type species of the genus. In summary, the fossil appears to have been a species with the body size of a medium or small mallard, but with heavier legs, and definitely smaller wings. It seems, therefore, to have been a sedentary bird, active in swimming and walking, but with slight necessity for prolonged use of the wings, since so far as known it had no resident predators. The general condition resembles what I found in study of the living Laysan duck, *Anas laysanensis* Rothschild, restricted to tiny Laysan, an island in the Hawaiian Wildlife Reservation that is only one and three-quarters miles in length. The ducks are restricted to the central salt-water lake where they range mainly around fresh-water seepages along the lagoon shore. When I approached they waddled slowly away, and took to wing rather heavily only when hard pressed. On Laysan, as on the Bermudas, there are no active predators so that strength in escape flight was not required. Some of the ducks flew fairly well over the lagoon, but others were exhausted after a flight of 125 yards so that I ran them down on foot and caught them by hand. It may be thought that the Bermuda duck was of similar habit.

The osteological differences that separate the fossil from living Anatinae are considerable, and may warrant its designation in a distinct genus, particularly since it appears to have no close relatives, either living or fossil. Most of the fossil ducks that may be related have been described from fragmentary bones, so that their full characters are unknown. Because of this it has seemed best for the present to treat the bird of Bermuda as a species of the genus *Anas* in the broad sense, at least until the osteology of all of the living kinds included in the subfamily is more fully known.

MEASUREMENTS OF *Anas pachyscelus* (IN MILLIMETERS)

Tarsometatarsus:

Length, 44.5, 44.9, 45.6, 45.7, 45.7, 45.8, 45.9, 45.9, 46.0, 46.2, 46.2, 48.2.

Transverse breadth of anterior end, 9.5, 10.0, 10.1, 10.1, 10.2, 10.2, 10.5.

Transverse breadth of shaft near center, 4.4, 4.5, 4.5, 4.6, 4.7, 4.7, 4.7, 4.9, 5.0, 5.1, 5.2, 5.3, 5.3.

Transverse breadth of distal end, 10.8, 10.8, 10.9, 10.9, 11.1, 11.3, 11.5, 11.8.

Tibiotarsus:

Smallest transverse breadth of shaft, 3.8, 4.0, 4.2, 4.3, 4.3, 4.4, 4.4, 4.5, 4.5, 4.5, 4.6, 4.6, 4.7, 4.7, 4.7.

Transverse breadth across condyles, 9.1, 9.1, 9.2, 9.2, 9.3, 9.3, 9.4, 9.4, 9.7, 9.9.
Femur:

Length, 48.0, 48.6, 52.3, 52.3, 52.4.

Transverse breadth through head, 11.6, 12.0, 12.2, 12.6, 12.8.

Transverse breadth near center of shaft, 4.6, 4.7, 4.8, 4.9, 4.9, 5.0, 5.1, 5.3, 5.3, 5.3, 5.3, 5.4, 5.4, 5.4, 5.6, 5.6, 5.6.

Transverse breadth through condyles, 11.2, 11.6, 12.0, 12.1, 12.5, 12.5, 12.6, 12.7, 12.8, 13.4.

Humerus:

Length, 83.8, 85.6, 87.5, 88.7, 90.1, 90.2.

Transverse diameter of proximal end, 19.3, 19.6, 19.7, 19.8, 19.8, 21.0.

Transverse diameter near center of shaft, 6.6, 6.8, 6.9, 7.0, 7.1, 7.3, 7.4, 7.5, 7.5, 7.7.

Transverse diameter through condyles, 13.3, 13.5, 13.6, 14.0, 14.4, 14.4, 14.4, 14.6.

Ulna:

Length, 68.9, 74.5.

Carpometacarpus:

Length, 53.6, 53.8, 54.2, 54.4, 58.0.

Height through metacarpal I, 12.5, 12.7, 12.8, 12.8, 13.0, 13.2, 13.7.

Length of intermetacarpal space, 27.7, 28.7, 29.5, 31.9.

Coracoid:

Length from head to internal distal angle, 47.9, 48.2, 49.8, 49.8, 49.9.

Smallest transverse diameter of shaft, 5.0, 5.0, 5.0, 5.1, 5.1, 5.2, 5.2, 5.3, 5.3, 5.6, 5.6, 5.8, 6.0, 6.1.

Family GRUIDAE, Cranes

BAEOPTERYX gen. nov.

Characters.—Differs from *Grus* Pallas, 1766, in form of the bones of the wing: Humerus with the head relatively narrower, the deltoid crest reduced in length, with considerably restricted area for muscle attachment; distal end with the points for tendinal attachment much weakened, and the processes in general relatively reduced in size; carpometacarpus with the bulk and strength found in modern *Grus canadensis* (Linnaeus), but length decidedly less; ulna with points for attachment of tendon and muscle reduced.

The type is *Baeopteryx latipes* sp. nov.

BAEOPTERYX LATIPES sp. nov.

(Pl. 2, figs. 1, 2; pl. 3, figs. 1-3)

Holotype.—U.S.N.M. No. 22505, right tarsometatarsus, from H. Bernard Wilkinson Quarry, south and west of Coney Island, Hamilton Parish, Bermuda.

Characters.—Tarsometatarsus similar to that of modern *Grus canadensis* (Linnaeus), but relatively heavier; shorter than in the small

subspecies *Grus canadensis canadensis*, but entire bone broader and stronger, with the distal end larger; trochlea for digit 2 larger; trochlea for digit 4 broader, with distal articular surface shorter; facet for articulation of digit 1 broader and larger.

The material at hand includes several broken tarsometatarsi as follows: Right side, proximal end 9, distal end 3; left side, proximal end 6, distal end 6; and 7 fragments from the central section of the shaft. These show agreement with the type in the characters noted.

Pedal phalanges.—These, part for part, are heavy compared to those of *Grus canadensis*, and so support the supposition of a stronger foot.

Tibiotarsus.—This segment is represented by fragments as follows: Right side, proximal end 8, distal end 5; left side, proximal end 6, distal end 3; and 8 sections from the central part of the shaft. The bone is strong, though it appears less heavy proportionately than the tarsometatarsus. Its main peculiarity is found in the tubercle that projects at the outer side of the lower end of the tendinal bridge which is narrow, somewhat elongated, and more smoothly rounded than in the modern cranes. Other parts of this bone, particularly of the proximal end, are too poorly preserved to offer characters useful in comparison.

Fibula.—One, nearly entire, appears relatively large, thus indicating the greater proportionate size of the leg.

Femur.—There are two nearly perfect; four fragments from the right side, and seven fragments from the left. Compared to *Grus canadensis* these are short and relatively heavy, with the internal condyle especially strong, and extended farther (downward). When the bone is viewed from the distal end the upper margin of the intercondylar fossa is more abruptly and more deeply grooved on the inner side. In the points of difference indicated the fossil is generally more similar to the much larger modern *Anthropoides paradisaica* (Lichtenstein) than to *Grus canadensis*.

Humerus.—This is represented by proximal and distal ends, and part of the shaft of another specimen, all from the right side. The bone, relatively, is small in size, with the head narrowed and the deltoid crest much reduced both in length and in the area of muscle attachment. The proximal end as a whole, compared with that of living cranes, is reduced, this feature including the upper section of the shaft. The line of insertion of the latissimus dorsi is strongly marked, the pneumatic opening, elevated in the usual position, is rather small, and the lower external margin of the bicipital crest is sharply angular. The reduction in size is evident also on the distal

end of the bone, where the tendinal attachments are weakened, a condition noted in the scar for the pronator brevis, in the flattened face of the entepicondylar prominence, and in the area of the ectepicondyle.

The form of the humerus as a whole is definitely that of a bird of reduced volant ability, notable particularly in a group of birds whose living species are strong in flight.

Ulna.—The material includes six proximal and six distal ends, with two additional segments of the shaft. These fragments corroborate the character of humerus and carpometacarpus in evident reduction in size. In addition the impression for the brachialis anticus, and the development of the other parts of the head are less in size and strength, characters that are repeated in relative form at the distal articulation. Though the reduction is less marked than in the wing elements on either side the indication is that of lesser power. The weakened papillae for attachment of the secondaries in particular give this impression. As the material is fragmentary, no definite measurement of the total length is available.

Radius.—The only part preserved is a section from the distal end, which indicates a reduction in size with a definite flattening of the shaft.

Carpometacarpus.—The eight specimens, three from the right side and five from the left, show the characters of this bone fully (except for the distal half of metacarpal III which is missing), and verify fully the supposition of reduction in powers of flight in this interesting species. The bone as a whole retains the bulk and strength found in living *Grus canadensis* but is only four-fifths as long. This shortened length has come in the distal area as the proximal end is as large as in the modern species with the parts of equal size and development. The reduction is evident particularly in the length of the shaft between the head of the bone and the proximal end of the intermetacarpal opening, and in length from the opposite end of the same open space and the distal margin of the bone, this being only half the length of the modern bird.

Second digit of first phalanx.—The single complete bone is about one-third shorter than in small *Grus canadensis*, though it is nearly as high in its central area. The details of form otherwise are like those in the larger bird.

The lessened length is another indication of the shortened wing.

Coracoid.—One nearly complete bone and three fragments indicate clearly a considerable reduction in size in this area of the skeleton.

The one nearly entire is shorter than a small specimen of the smallest of the living subspecies of *Grus canadensis*, and is decidedly less in size of shaft and in extent of the broadened end that articulates with the sternum. A size one-fourth less at least is demonstrated, which by analogy would be found likewise in the sternum. The smaller dimension would affect the size of the breast muscle, so that the coracoid is further indication of lessened ability in flight.

Scapula.—The articular ends of several show no details of significant difference.

Vertebrae.—Several that are nearly complete are of the type usual in cranes.

Skull.—The few fragments consist of the end of one premaxilla with the tip broken, three symphyses of the mandible with the tips missing, and the articular, and immediately adjacent, parts from the left side of the lower jaw. The robust size of these is surprising as they are equal to the larger subspecies of the brown crane *Grus canadensis tabida*, while the other dimensions in the skeleton, except for the heavy foot, are generally less than those of the smaller race *Grus canadensis canadensis*.

Remarks.—The material of this species is sufficient to give a general outline of the form of the bird, which is seen to be somewhat less in stature than the smaller race of the living sandhill crane *Grus canadensis canadensis*, though coupled with this is a shorter wing, a heavier leg, seen particularly in the foot, and a larger head.

A survey of the species of the family Gruidae that have been recognized in fossil form indicates only two that require brief comment. *Grus conferta* Miller and Sibley from the late lower Pliocene of California, recorded from the distal end of a tarsometatarsus, is a much larger bird than *Baeopteryx latipes*, as the type specimen has the size of the modern whooping crane *Grus americana*. Another species from the middle Pliocene of Kansas, *Grus nannodes* Wetmore and Martin, described from a carpometacarpus, perhaps had about the same body size as the species from Bermuda, but agrees in form of the type bone with *Grus canadensis* and thus is different.

The weakened wing structure of the Bermudan species, indicative of considerably reduced power of flight, is so different from that of modern cranes as to justify separation in a genus distinct from *Grus*. The name *Baeopteryx* is taken from the Greek βαίός, small and πτερυξ, wing. The specific name is from the Latin *latus*, broad, and *pes*, foot.

MEASUREMENTS OF *Baeopteryx latipes* (IN MILLIMETERS)

Tarsometatarsus:

Length, 184.

Transverse breadth of anterior end, 22.6, 22.6, 23.5, 23.6, 23.9.

Transverse breadth of shaft near center, 8.0, 8.0, 8.3, 8.3, 8.5, 8.6, 8.8, 9.1.

Transverse breadth of distal end, 20.4, 20.8, 22.4, 22.7.

Tibiotarsus:

Smallest transverse breadth of shaft near distal end, 9.9, 9.9, 10.4, 10.5.

Transverse breadth across condyles, 19.1, 19.8, 20.2, 20.9, 21.0, 21.5.

Femur:

Length to distal end of internal condyle, 98.2, 100.8.

Transverse breadth through head, 23.0, 23.7, 24.3, 24.8.

Transverse breadth near center of shaft, 10.2, 10.5, 10.7, 11.0, 11.0, 11.4, 11.5.

Transverse breadth through condyles, 22.0, 22.2, 23.2, 23.7.

First phalanx of third toe:

Length, 29.0, 29.4, 29.8, 31.6.

Humerus:

Transverse diameter of proximal end, 33.5.

Transverse diameter near center of shaft, 12.4, 13.1, 13.4.

Transverse diameter through condyles, 25.6.

Carpometacarpus:

Length, 79.0, 79.7, 79.9, 80.1.

Vertical height through metacarpal I, 20.3, 20.5, 20.8, 21.1, 21.3, 21.6.

Length of intermetacarpal space, 41.5, 42.0, 42.6, 43.8, 44.6.

First phalanx of digit 2:

Length, 34.7.

Vertical height near center, 11.3.

Coracoid:

Length, from head to inner distal angle, 54.0.

Transverse width of shaft at narrowest point, 10.0

Family RALLIDAE: Rails

The collection contains various bones from four species of rails, one very small, two of intermediate size, and one nearly as large as the modern clapper rail. These are not clearly marked in the present collection so that no attempt is made to describe them here in detail, particularly since complete material for one of them is now in other hands for study.

EXPLANATION OF PLATES

PLATE 1

Leg and wing bones of a duck, *Anas pachyscelus*, from the Bermuda Pleistocene

- Fig. 1. Palmar and anconal views of right humerus, natural size.
- Fig. 2. Outline views of left femur, natural size.
- Fig. 3. Left tarsometatarsus (type), natural size.
- Fig. 4. Left coracoid, natural size.
- Fig. 5. Right carpometacarpus, natural size.

PLATE 2

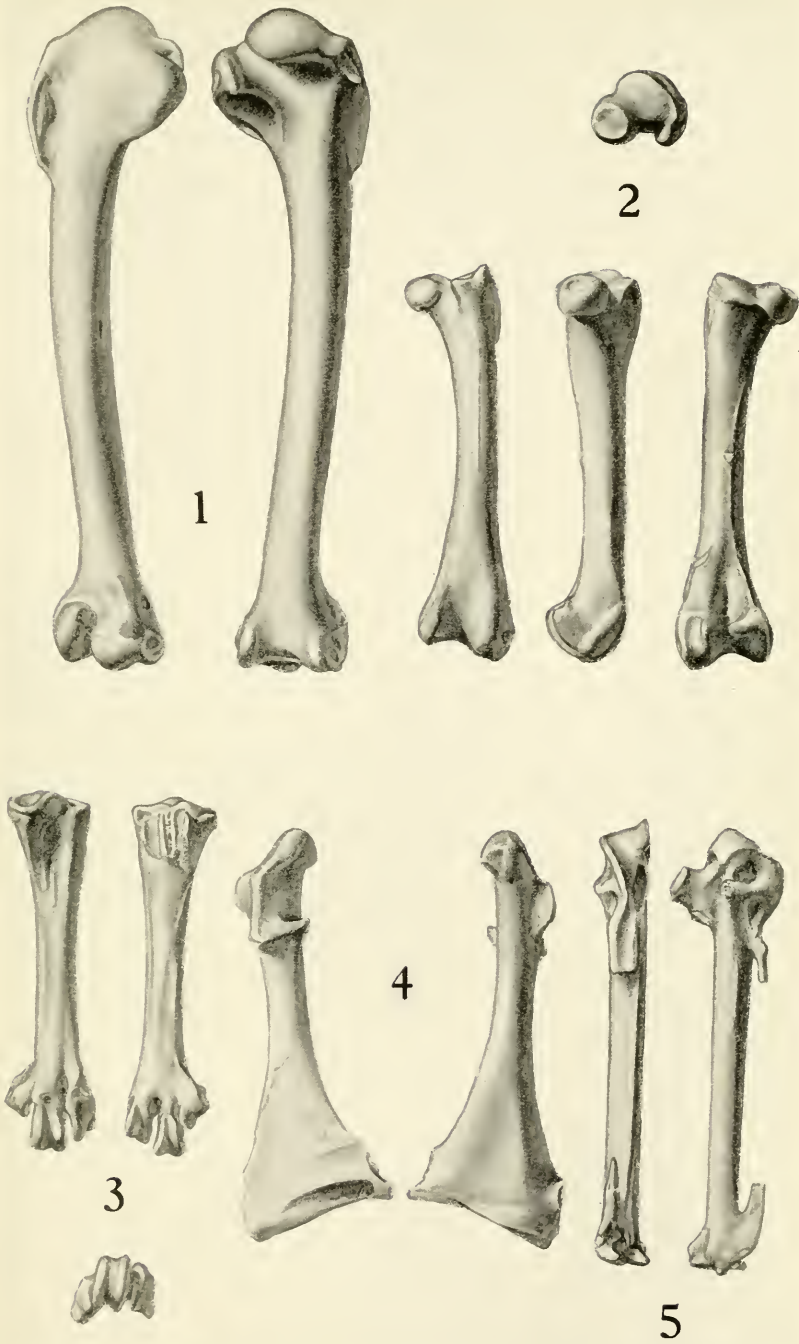
Leg bones of a crane, *Bacopteryx latipes*, from the Bermuda Pleistocene

- Fig. 1. Right tarsometatarsus (type), natural size.
- Fig. 2. Femur, natural size.

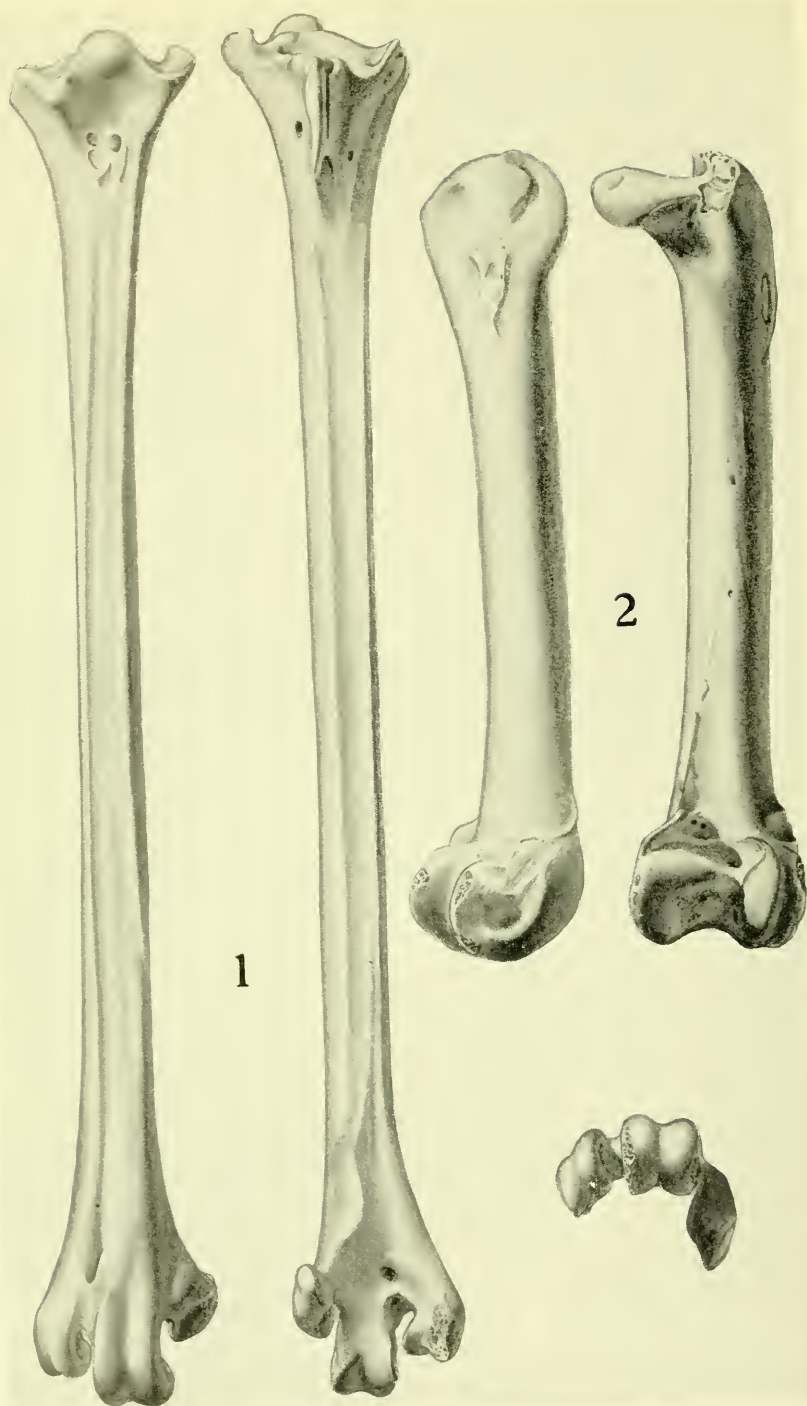
PLATE 3

Wing bones of a crane, *Bacopteryx latipes*, from the Bermuda Pleistocene

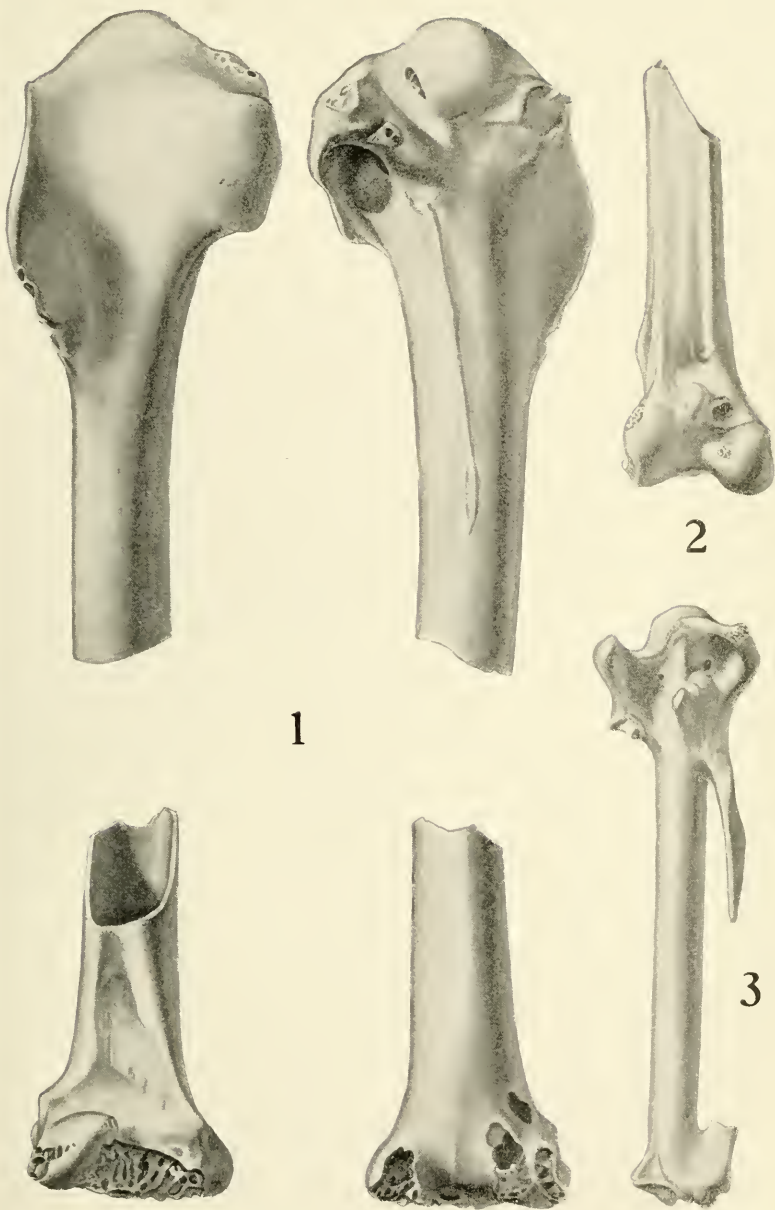
- Fig. 1. Humerus, natural size.
- Fig. 2. Distal end of tibiotarsus, natural size.
- Fig. 3. Carpometacarpus, natural size.



(See explanation of plate at end of text.)



(See explanation of plate at end of text.)



(See explanation of plate at end of text.)



SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 140, NUMBER 3

DOCTOR LANGLEY'S PARADOX: TWO
LETTERS SUGGESTING THE
DEVELOPMENT OF ROCKETS

(WITH THREE PLATES)

By
RUSSELL J. PARKINSON

Museum Aide, National Air Museum, Smithsonian Institution; and
Instructor of History, Duke University



(PUBLICATION 4424)

CITY OF WASHINGTON
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*Museum Aide, National Air Museum, Smithsonian Institution; and
Instructor of History, Duke University*

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Two previously unpublished letters written in 1902 by Samuel Pierpont Langley, third Secretary of the Smithsonian Institution, have recently been uncovered in the "Langley Documents on Aerodromics" held by the National Air Museum, Washington, D. C. These letters not only anticipated the development of powered flight, which Langley considered a certainty, but also demonstrated that Langley's far-ranging mind had foreseen even the development of the modern rocket.

Plagued by many problems, including the need to obtain a gasoline engine of sufficient horsepower in relation to its total weight, Langley had suffered innumerable delays in constructing an "aerodrome" or flying machine intended to carry a man. After several years of disappointment, and with some hesitation, he permitted his young assistant, Charles M. Manly, to undertake the rebuilding of an unsuccessful Balzar engine.¹ Using a revolutionary principle of placing steel jackets around cast-iron cylinder walls, Manly soon built an engine which produced over 52 horsepower, the net weight of the engine proper being only 2.4 pounds per horsepower. The success of the "aerodrome" seemed assured.

Langley's spirits revived, and his correspondence during the spring and summer of 1902 indicated a renewed interest in the construction of his large flying machine. A whole new realm of aeronautical possibilities formed in his mind, and he discussed these ideas among the small group of friends and associates in whom he could confide. Fortunately for history, it was Langley's custom to record the

* This article was completed with the cooperation of the staff of the National Air Museum.

¹ Built by Stephen M. Balzar of New York, it failed to meet the specifications of producing 12 horsepower while weighing less than 100 pounds.

essence of his ideas and conversations in "Waste Books," and he would occasionally confirm these by letters to the persons involved.

On one occasion after visiting with Manly, Langley returned to his office and there on March 9, 1902, wrote:

DEAR SIR:

It occurs to me to take a note of what I said to you on Saturday, the 8th instant, in the upper shop of the South Shed,² though it is of no immediate practical use. It is that the ultimate development of the flying machine is likely to be an affair of very small wings or no wings at all, and that it may depend for its velocity on what Mr. Bell³ calls 'its momentum' in the same way that an arrow or any other missile flies. It is known that the arrow derives its energy from the bow which projects it and that when this is spent the arrow will drop. We have, however, only to renew this energy and when renewed the source is immaterial and the result is the same, wherever the energy originates, for the arrow may still be heading upward without limit, as in the case of a rocket which has no wings but goes very much better without them, renewing its energy by recoil. Here is an additional analogy for the success of the greatest soaring birds with small wings. In any case it is a thing which deserves thinking over.

Very respectfully yours,
(signed) S. P. LANGLEY,
Secretary.

MR. C. M. MANLY
Aid in Aerodromics
*Smithsonian Institution*⁴

Did experimenters in aeronautics turn first to the development of the wrong types of aircraft? For centuries the graceful flight of the birds had called men like a Lorelei. While the balloon and airship offered a cumbersome solution to the age-old search for a device with which men might rise into the air, it was the secret of lift on sustaining surfaces, the secret of the soaring birds, which gave men the clue for the airplane. In 1902 Langley, while developing the large aerodrome, was also engaged in a project of photographing birds in flight and preparing a study based upon information obtained. Then this concept of a rocket thrust itself into his versatile mind. Now we know that scientists have developed the idea of a rocket beyond the stage of "thinking over" and into the stage of practical use. As

² The South Shed is a small frame building in which the Langley Aerodromes were constructed. It is on the Independence Avenue side of the Smithsonian Institution Building and is now used as a cabinet shop.

³ Alexander Graham Bell, a Regent of the Smithsonian Institution, and supporter of aeronautical activities, using his fortune amassed through the invention of the telephone.

⁴ Langley to Manly, March 9, 1902, "Board of Ordnance and Fortification Correspondence Book No. 4, October 15, 1901-October 9, 1906," p. 26; *Langley Documents on Aerodromics*, vol. 30. National Air Museum.

Langley viewed the solution of an aeronautical problem, the answer was to be found in the power-plant and the application of that power. This factor of power is more than ever a part of scientific rocket research. The development of flight had awaited the development of a light-weight engine which could be harnessed to propellers and pull or push sustaining surfaces or wings through the air to create lift and, hence, flight. Langley designed and built his "aerodrome" using sustaining wings. Then on September 25, 1902, while on a trip to Boston, he again opened his mind to Manly. Langley acknowledged a telegram from Manly and noted that Maxim⁵ would not enter his engine for the prize offered by the St. Louis Exposition of 1904. He then concluded with this paragraph:⁶

I have been thinking of something so paradoxical that I hesitate to enunciate it even as a mere possibility. The very idea of the aerodrome as we have always conceive [sic] it, has been to obtain support from sustaining surfaces driven against the air. I seem to see my way to dispensing with the surfaces absolutely and altogether so long as the engine works. I do not mean that this is a hypothetical possibility, but something apparently practical and perhaps within our actual means, or very near it. It is one of the very simple things which we both know are the last to be seen, but I will write to you or better talk to you about this later.

If Langley had any further thoughts on the possibility of wingless aircraft he must only have spoken of them to Manly; there is apparently no further correspondence between them on this subject. Upon his return to Washington Langley did, however, pursue the subject one step further. In a memorandum dated October 14, 1902, he recorded the conversation in which:

I submitted to Professor Newcomb⁷ today the following question, using concrete values "to fix our ideas."

A spherical rocket head, which weighs 20 pounds, is initially maintained in place by a vertical pressure of 20 pounds caused by reaction and due to a force which we may suppose, for illustration, to be 1 horsepower.

Next, let us suppose the axis of the reactive jet still to be directed to the centre of gravity of the head, but at some acute angle α with the horizon.

I understand that the rocket will advance indefinitely in a horizontal line with accelerated velocity under the impulse of a constant force $\frac{1}{\sin \alpha}$ being 2 horsepower producing 40 pounds.⁸

⁵ Sir Hiram Maxim, who had conducted aeronautical experiments in England in 1894.

⁶ Langley to Manly, Boston, Mass., September 25, 1902, *op. cit.*, p. 152.

⁷ Prof. Simon Newcomb, mathematician and astronomer who for many years was associated with the Nautical Almanac and the U. S. Naval Observatory.

⁸ Added to the original copy, in handwriting believed to be Langley's, "in case $\sin \alpha = \frac{1}{2}$."

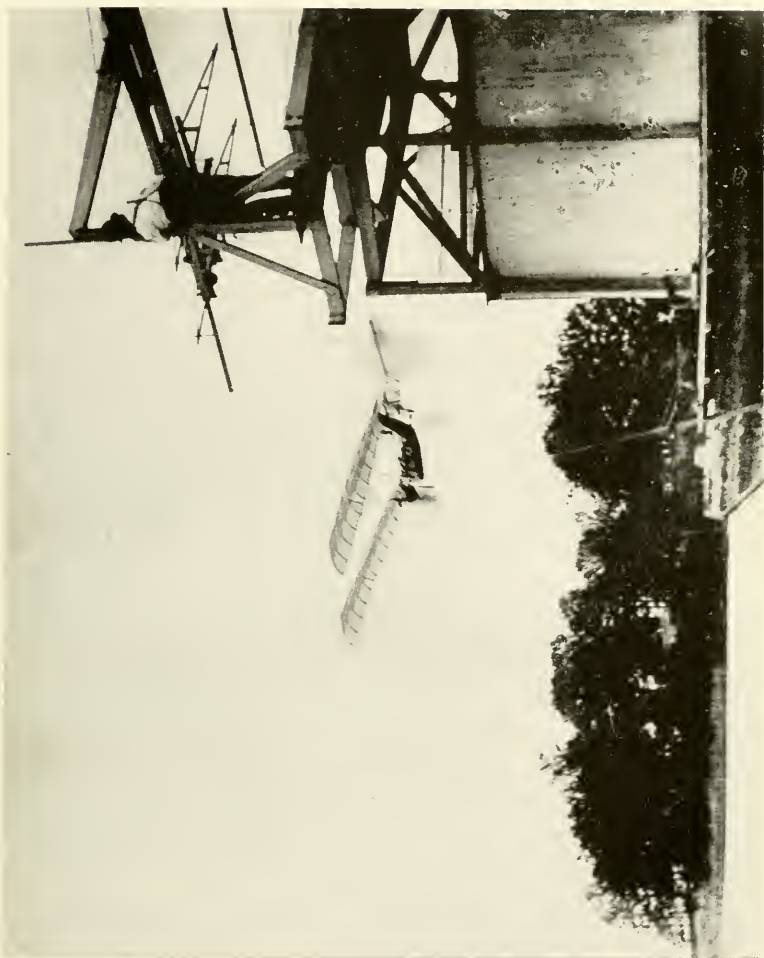
Am I right in supposing that it would move with a constant acceleration in this horizontal line until the resistance of the air caused the motion to be constant, and what would this velocity approximately be when it became so? ⁹

Was this only a theoretical problem to help solve a problem concerning the construction of the "aerodrome," or was this new problem an insight into the development of aviation or astronautics as power-plant efficiency increased? The historian may only speculate upon what new experiments Langley would have begun had the "aerodrome" proved to be successful, but its failure and the resultant criticism crushed an inventive soul.

Today, the occupant of the office where Langley once spent so many hours can look out of his window and see two new sentinels standing watch at the Smithsonian. Beside the old Arts and Industries Building a United States Army Jupiter C and an Air Force Atlas remind the constant stream of visitors of new accomplishments in the story of aeronautical and astronautical progress. In the morning sun the shadows of these towering monuments point like an arrow to the gray-shingled South Shed only a short distance away. Dr. Langley's paradox has been fulfilled.

⁹ Memorandum, October 14, 1902, Smithsonian Files; Letters Written; Aerodromics 20, vol. 9 (May 25, 1902, to Feb. 9, 1904), p. 35.

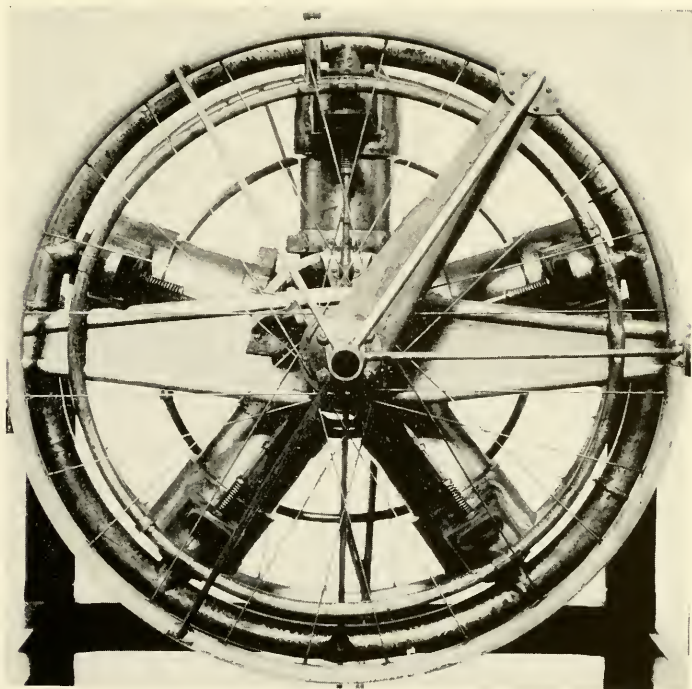
PLATES



The successful launching of Langley's unmanned "Aerodrome No. 5" on May 6, 1896. Driven by a 1-horsepower steam engine, the "Aerodrome" had a wingspan of nearly 14 feet. This experiment proved the practicability of powered flight.



Professor Langley (at right) and Charles M. Manly, just before launching the "Aerodrome," October 7, 1903.



1. The Manly engine.



2. The engines of a U. S. Air Force Atlas launching vehicle, photographed as the vehicle arrived for display at the Smithsonian Institution, 1960.



SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 140, NUMBER 4

THE CEPHALIC NERVOUS SYSTEM
OF THE CENTIPEDE ARENOPHILUS
BIPUNCTICEPS (WOOD) (CHILOPODA,
GEOPHILOMORPHA, GEOPHILIDAE)

(WITH FIVE PLATES)

By
MICHAEL A. LORENZO
Woodstock College
Woodstock, Md.



(PUBLICATION 4425)



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THE CEPHALIC NERVOUS SYSTEM OF THE CENTIPEDE *ARENOPHILUS BIPUNCTICEPS* (WOOD) (CHILOPODA, GEOPHILOMORPHA, GEOPHILIDAE)¹

By MICHAEL A. LORENZO
Woodstock College, Woodstock, Md.

(WITH FIVE PLATES)

I. INTRODUCTION

This paper deals primarily with the gross and microscopic anatomy of the cephalic nervous system of a geophilomorphous centipede. In contrast to the voluminous literature concerned with the neuroanatomy of other arthropods, little work has been done on the class Chilopoda, and virtually nothing is known about the order Geophilomorpha. Inasmuch as valid interpretations of phylogenetic relationships must be based on the varied studies of numerous workers, a knowledge of the neuroanatomy of this hitherto neglected group is desirable.

GENERAL CONSIDERATIONS

Centipedes are terrestrial arthropods which lead a cryptozoic existence. Nocturnal habits and dark hiding places during the day make their biotic presence unfelt. They exercise little influence on man's economy and have eluded the interest of most biologists. The chilopods, however, are regarded with reverential fear by many of the lower organisms, especially the insects. Characteristically they possess prehensors, which contain a poison gland. Unlike their myriapod kin, the millipedes, they are carnivorous and rapid runners. Predaceous even to the habit of cannibalism, centipedes are capable of inflicting fatal "bites," and some mammals have succumbed to their attack. There are many exaggerated tales of their attacks on the human species. Some of the larger scolopendromorphs² of the eastern world, however, attain the formidable length of over 12 inches; and the death

¹ The research for this paper was completed at St. Louis University, St. Louis, Mo.

² *Scolopendra gigantea*.

of several human beings, indeed, has resulted from the venom injected by their poison claws. Less common is the morbidity known as chilopodiasis, which is the invasion of a sinus by a centipede.³ As a zoogeographical fact, however, western civilization is spared all but the occasional horror of seeing *Scutigera*, the common house centipede, caught by surprise running across a tile floor.

The Chilopoda are recognized as a class of the phylum Arthropoda and include only the opisthogoneate centipedes, which bear one pair of legs per segment. The progoneate millipedes, easily distinguished by the presence of two pairs of legs per segment, belong to the class Diplopoda. At one time both classes were grouped together in the Myriapoda, a term erected by Latreille in 1802, but, though still in use, it no longer has taxonomic status.

All centipedes fall into one of two classes: Notostigmophora and Pleurostigmophora (Verhoeff, 1925) or Anamorpha and Epi-morpha (Attems, 1926). The classificatory schemes of three taxonomists serve to define the position of the Geophilomorpha and will be of historical as well as systematic interest. Pocock (1902) considered the Geophilomorpha the most primitive stock and gave the following classification:

Subclass Pleurostigma.

Orders:

Geophilomorpha.

Scolopendromorpha.

Craterostigmophora.

Lithobiomorpha.

Subclass Notostigma.

Order Scutigermorpha.

Stressing the importance of an embryological character not known to Pocock, Verhoeff (1925) further refined the classification by erecting two superorders in the Pleurostigmophora. His scheme is inverted to reflect the primitive condition of the Scutigermorpha. The summary of his classification is as follows:

Subclass Notostigmophora.

Order Scutigermorpha.

Subclass Pleurostigmophora.

Superorder Anamorpha.

Orders:

Lithobiomorpha.

Craterostigmophora.

³ Wilson (1929) gives the history of a patient who sneezed an arthropod into his handkerchief, promptly relieving a nasal congestion of several years. The article erroneously refers to the organism as an insect, but the photograph clearly identifies it as a geophilomorph.

Subclass Epimorpha.

Orders :

Scolopendromorpha.

Geophilomorpha.

Count Carl von Attems (1926), however, makes several modifications. He does not consider the Scutigermorpha worthy of subclass rank on the basis of its gross anatomical features alone but respects the embryological evidence as justifying his division of the order into the subclasses Anamorpha and Epimorpha. He further relegates the Craterostigmophora to subordinal rank. His is the following classification :

Subclass Anamorpha.

Orders :

Scutigermorpha.

Lithobiomorpha.

Suborder Craterostigmophora.

Subclass Epimorpha.

Orders :

Scolopendromorpha.

Geophilomorpha.

The classification of Attems appears to be the more natural and is the scheme which we have adopted for our discussion in the light of the following evidence :

Anamorpha.—Postembryonic development is by hemianamorphosis—that is, the young leaves the egg with only seven fully formed trunk segments and seven pairs of legs ; the eggs are laid singly by the parent female and she broods neither the eggs nor the young. The adults of both orders possess 15 pairs of ambulatory appendages. The Scutigermorpha is the only order of the class possessing compound eyes, and the external respiratory openings (stomata) are dorsally situated and unpaired. The Lithobiomorpha have simple ocelli, when visual elements are present, and the external respiratory openings (stigmata) are lateral and paired.

Epimorpha.—Postembryonic development is by epimorphosis—that is, the young animal leaves the egg with the adult complement of pedal segments and pairs of legs ; the eggs are laid in groups, and the female broods both the eggs and the young. The Scolopendromorpha have either 21 or 23 pairs of walking legs, and this number is constant within the species. The antennae have at least 17 articles. The Geophilomorpha, on the other hand, possess no less than 31 pedal segments and may number as high as 183 with intraspecific variation.⁴ The antennae constantly have 14 articles.

⁴ It should be remarked that, exclusive of the prehensors, the number of pairs

The order Geophilomorpha includes 10 families and over 120 genera. Typically a long, vermiform arthropod, geophilomorphs are found under rocks, in loose soil and forest litter, under the bark and in the wood of decaying trees, and occasionally under drying dung hills. They share with their chilopod relatives the outdoor life and cryptozoic customs. The geophilomorphs have neither ocelli nor Organs of Tömösvary. The antennae are the principal sense organs of the head. The body tergites, unlike those of the other chilopod orders, are homonymous. A single pair of mandibles, first and second maxillae, comprise the mouth parts, which are in part concealed by strongly developed prehensors. With the exception of the anterior and posterior extremities of the animals, the trunk is a repetition of almost identical segments. Each body segment has its own ganglion joined to its neighboring ganglia by paired connectives. The ganglia and connectives comprise the ventral nerve cord. The alimentary canal is a long continuous tube beginning at the mouth and ending in an anal opening on the terminal body segment. A pair of Malpighian tubules empties into the hind gut. There is a single elongate testis in the male and paired seminal vesicles which communicate at the single genital opening located ventrally on the penultimate segment. The female reproductive organs are similarly an unpaired ovary, paired ducts, and a single opening situated on the penultimate segment.

Arthropod neuroanatomy.—Since the chilopod nervous system follows the pattern of that of the typical arthropod, a brief review of the structure of the brain and nerve cord will not be without profit.

The neurons, the essential cellular components of nerve tissue, are grouped together into masses called ganglia. The axons of these cells emerge from the ganglia as nerves, or course within the ganglia as fiber tracts. Other cells are present in the ganglia which are non-nervous supporting elements. These are called neuroglial cells, or simply neuroglia. The axons of invertebrates are generally considered to be nonmedullated, but there is present a submicroscopic lipoprotein sheath not unlike myelin. The central nervous system and the emerging nerves are clothed in a connective tissue covering composed of an acellular "neural lamella" and a cellular "perilemma." The two are referred to as "neurilemma."⁵

of walking legs in all centipedes is never an even count. A tentative explanation for intraspecific variation in the Geophilomorpha is that segments may be added in successive molts and that variation in pedal counts may be a function of age. (Crabill, private communication.)

⁵ The term "neurilemma" is used differently by mammalian histologists.

Typically there is a pair of ganglia for each body segment but, in most of the arthropods, the pair is fused. The ganglia are interconnected by longitudinal and transverse connectives and commissures respectively. In the higher insects the ganglia of adjacent segments are so concentrated as to be indistinguishable as individual entities. This coalescence reaches an extreme in the Diptera, where the single thoracic ganglion is in reality an amalgamation of many segmental ganglia.

Transverse sections reveal the typical ganglion as being composed of an inner core of nerve fibers, termed the neuropile, and an outer cortex of neurons. This arrangement is the reverse of that found in the vertebrate spinal cord, where the fibers are located in the cortical white matter, and the nerve cells in the medullary gray matter. Since sensory neurons are situated in the epidermis, the neurons contained within the central nervous system are either motor or internuncial in nature, and are typically unipolar. Multipolar and bipolar cells are found in the vicinity of the receptors. Within the fibrous neuropile are found varying amounts of neuroglial cells.

The central nervous system consists of a brain, or supraesophageal ganglion, the subesophageal ganglion, and the ventral nerve cord. The brain is the dorsal aggregation of nerve tissue in the cephalic capsule situated either anterior or dorsal to the esophagus, depending on the shape of the head. According to the terminology of Viallanes (1887), the brain is divided anatomically into three regions known as the protocerebrum, deutocerebrum, and tritocerebrum. The regions, however, are not always clearly defined externally. In most insects the greater portion of the protocerebrum is associated with the visual apparatus. Where eyes are absent or poorly developed, this region is reduced.⁶ The protocerebrum is further divided into protocerebral lobes and optic lobes. The second region of the brain, the deutocerebrum, innervates the antennae. For the most part, it is sensory and internuncial in function but may contain some motor elements associated with the antennal musculature. Efferent fibers may emerge from the antennal lobes independent of the sensory roots and are sometimes called accessory antennal nerves. The third region, the tritocerebrum, is represented as the ventral portion which communicates directly with the subesophageal ganglion by way of the circumesophageal connectives. It is through the tritocerebrum that the central nervous sys-

⁶ Power (1946a) has found that, although quantitative differences exist, there are no detectable qualitative architectural modifications in the brain of eyeless *Drosophila* mutants. There is no correlation between the inability to see with a qualitative hypoplasia of the central nervous system.

tem makes connection with the stomatogastric, or "sympathetic," nervous system. A pair of lateral roots emerges from the tritocerebrum and enters what appears to be the central center of the stomatogastric system, the unpaired frontal ganglion. It is from this ganglion that the median recurrent nerve emerges.

The subesophageal ganglion innervates the mouth parts and contains both motor and sensory components. There are often present in this ganglion "giant cells," which are specialized nerve cells with neurosecretory significance. The subesophageal ganglion communicates with the supraesophageal ganglion by means of the circumesophageal connectives, which circumvent the esophagus and may be notably long or almost nonexistent. In the latter case the brain appears to adjoin the subesophageal ganglion directly.

ACKNOWLEDGMENTS

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II. REVIEW OF THE LITERATURE

Investigations of the chilopod nervous system began early in the 19th century (Treviranus, 1817; Leon-Dufour, 1824). Until methods of microtomy were introduced in the second half of that century, studies were confined to gross dissections and a few *in toto* staining procedures. The smaller species of centipedes and the Geophilomorpha were given very little attention.

Newport (1843) was the first worker to study the nervous system of a geophilomorph (*Geophilus* [†] *subterraneus* Leach). Having recognized the importance of a comparative invertebrate neurology as "an aid in resolving problems of life in higher animals," Newport studied the abdominal ganglia of three chilopod types: a lithobiid, a scolopendrid, and a geophilid. He described the pedal nerves and the manner in which they emerged from the central ganglion. More noteworthy, however, is the footnote which appeared on page 245. He remarked that in the embryo of the geophilomorph *Necrophloeophagus longicornis* (Leach)—

[†] = *Stigmatogaster subterraneus* (Leach).

at the moment of bursting its shell, the brain is composed of four double ganglia, the centers of the corresponding number of segments, which are then becoming aggregated together to form the single movable portion of the head in the perfect animal; so that the brain of the myriapod, and probably of all the higher Articulata, is in reality, composed of at least four pairs of ganglia.

This was a precocious observation, for Newport was seeing for the first time in a geophilomorph the protocerebra, deutocerebra and tritocerebra of the brain and the subesophageal ganglion located in the cephalic capsule.

Saint Remy (1887), employing the microtechniques of Dietl (1876), was the first to make an intensive investigation of the centipede brain. Two geophilomorphs, *N. longicornis* and *S. subterraneus* (Leach), were studied in addition to other centipedes, various millipedes, araneids, and insects. Illustrations made from sectioned material appear in 14 plates containing 155 figures. His work is a notable contribution to the field of comparative invertebrate neurology. Several discrepancies, however, have been discovered in his work by other investigators (Hörberg, 1931; Fahlander, 1938), who, in demonstrating inaccuracies regarding other species, have jeopardized an appreciation of the exactness of his observation on the geophil brain. In the light of some of the more recent studies, Saint Remy's treatment of the brain of *longicornis* is brief; some of his interpretations are questionable. He described, for example, a small nerve emerging inferiorly from the posterior part of the frontal lobe (see pl. 6, fig. 68) and called it the "nerf de Tömösvary." Whether he mistook this nerve for one innervating the Organ of Tömösvary—which is lacking in the Geophilomorpha—or whether he considered it a vestigial homologue of the nerve to that organ in other centipedes, could not be determined by the present author.⁸

The paper of Crabill (1951) is of interest in that it suggests a close affinity of the species *N. longicornis*, studied by both Newport and Saint Remy, and the geophil selected for this study, *Arenophilus bipuncticeps* (Wood). While examining the four type specimens on which Meinert (1886) based the new species *Geophilus huronicus*, Crabill discovered that two of the centipedes are assignable to *longicornis*, a geophil widely distributed throughout Europe, and the others to the North American *bipuncticeps*. The four were considered conspecific by Meinert.

Although other workers have studied the chilopod nervous system (Child, 1892; Adensamer, 1893; Duboscq, 1899; Haller, 1905;

⁸ It is now known that this nerve innervates the "cerebral gland" and has neurosecretory significance (Gabe, 1952).

Holmgren, 1916; Verhoeff, 1925; Hanström, 1928; Hilton, 1930; Hörberg, 1931), it was not until Kjell Fahlander (1938) had completed his doctoral dissertation that geophilomorph neuroanatomy was again treated in the literature.

In a general treatment of the anatomy of representatives of the four orders of centipedes, Fahlander devoted a large portion of his research to a detailed study of the nervous system. He described more cephalic nerves than had hitherto been reported and homologized them on the basis of an intensive study of a scutigermorph, *Thereuopoda clunifera*. The cephalic ganglia and nerves of *Lithobius forficatus*, *Scolopendra cingulata*, and the geophilomorph from Japan, *Scolioplanes*⁹ *hirsutipes*, were described and clearly illustrated. The internal histology and disposition of fiber tracts were thoroughly investigated in the scutigermorph, but the geophilomorph was given little more than gross study. Fahlander's work encountered some opposition from the late G. F. Ferris (1953), but a critical review of both papers will reveal that Ferris had misunderstood Fahlander on several crucial points. The points of disagreement will be treated in another section of this paper.

A bibliography of the microscopic anatomy of the geophilomorph brain is nonexistent. Saint Remy (1887) describes briefly the cortical structure of the three neuromeres of the subesophageal ganglion. This is the only existing work known to the present author. It is necessary, therefore, to draw from the reports of workers on other arthropods (Hörberg, 1931; Snodgrass, 1935; Scharrer, 1939, 1941; Wigglesworth, 1953; Gabe, 1952; Imms, 1957; Hess, 1958).

Since the present investigation is concerned with the geophilid *Arenophilus bipuncticeps* (Wood), a brief resumé of the taxonomy of this organism is indicated.

The genus *Arenophilus* was created by R. V. Chamberlin (1912). A year later Gunthorp (1913) reported that *A. bipuncticeps* was common in Kansas. Crabill (1955) collected specimens of this species in three counties of Missouri and in eight localities in and around St. Louis. Johnson (1952), who studied the distribution of centipedes and millipedes in Michigan, gives the following synonymy:

Arenophilus bipuncticeps (Wood), 1912

Geophilus bipuncticeps Wood, 1862, Journ. Acad. Nat. Sci. Philadelphia, vol. 5 (ser. 2), p. 45.

Geophilus latro Meinert, 1870, Naturh. Tidschr., vol. 7 (ser. 3), p. 79.

Geophilus georgianus Meinert, 1885, Proc. Amer. Philos. Soc., vol. 23, p. 219.

Arenophilus bipuncticeps Chamberlin, 1912, Canadian Ent., vol. 44, p. 66.

⁹ = *Strigamia hirsutipes*.

III. MATERIAL AND METHODS

HISTOLOGICAL PROCEDURE

Specimens assignable to *Arenophilus bipuncticeps* (Wood) were collected in the late spring and summer in the vicinity of Florissant and Bellefontaine, Mo., when these arthropods were most abundant. Most of the centipedes were found under flat rocks which had a "good bite" on the ground. Some were collected under the loose bark of felled trees. It was found expedient to kill and fix the collections in the field, or soon after capture in the laboratory. Because of their cannibalistic habits, they were placed in individual containers along with some of their immediate environment when it was necessary to keep them alive. Sensitive to sudden changes in temperature and humidity, they are not amenable to culture.

A variety of fixatives was used. Dietrich's (Kahle's), Carnoy's, Sinha's (1953), Bouin's, hot alcohol, and cupric trinitrophenol were employed with varying degrees of success. A mixture (1:1) of aqueous and alcoholic Bouin's solutions was found to give best results antecedent to silver impregnation (see Bodian, 1937). The harsher fixatives (Sinha's, Carnoy's) required narcotization and were abandoned. The modification of Bouin's fixative was neither too slow nor too drastic and was used routinely.

A graded series of ethanol mixed with increasing volumes of n-butyl alcohol (Stiles, 1934) was used for dehydration of tissue previous to paraffin imbedding. Terpeneol (oil of lilac) was employed as a clearing agent. This did not harden the cuticular material so as to complicate sectioning. To facilitate infiltration the tips of the poison claws and the distal 10 or 12 antennal articles were excised with iridectomy scissors under the dissecting microscope.

The imbedding medium was prepared by melting together nine parts of Fischer tissue mat (60°-63° C.) and one part of bayberry wax. This mixture was heated over a low flame for several hours and filtered to insure better texture and cutting quality.

Material cleared in terpeneol required about five changes of fresh infiltration medium. When the odor of lilac is no longer detectable, infiltration is complete. Although heat hardens cuticle which has been treated with the more common clearing agents (i.e., xylol, toluol, etc.), terpeneol-cleared tissue left in the oven for over eight hours did not harden appreciably. Rapid infiltration in vacuo tended to distort and collapse material and was abandoned when the advantages of terpeneol were discovered.

Serial sections were cut with a Spencer rotary microtome. Dry ice

in a plastic funnel placed above the microtome blade and object carrier was used to lower the temperature during the actual microtomy. Because of the minute size of the material, crooked ribbons were almost useless. A device was designed to prevent this nuisance (Lorenzo, 1959), and it greatly improved the condition of the ribbon. Transverse, horizontal, and longitudinal sections were cut at 10 micra.

Albumenized water was used as an adhesive. One drop of Mayer's Egg Albumen was added to ten milliliters of distilled water. The water was first boiled to expel gases which might form bubbles under the sections. Because of the consistency of the imbedding medium, stretching of ribbons was kept to a minimum. The excessive adhesive was drained off, the slides were chilled briefly under dry ice, and gently blotted, face down, on filter paper. Drying was continued on the warming table for about an hour and completed in a desiccator before staining. The slightest trace of moisture under the sections caused loss of material in the subsequent steps of deparaffinizing and hydrating. After the paraffin had been removed from the tissue, 5-minute immersion in 0.1-percent celloidin followed by a brief (no longer than 60 seconds) drying in air was employed as an added precaution against section loss.

Hansen's trioxymethylene counterstained with picrofuchsin (Richins, 1938) was found to be a good general stain. Muscle tissue stains yellow, connective tissue and neurilemma red, and nuclei dark brown.

Several silver impregnation methods were tried without success. Controlling the pH of impregnation solutions (Samuel, 1953a; Peters, 1955) gave inconsistent results with the silver nitrate method of Holmes (1943). Both chilopod and vertebrate nervous tissue was affixed to the same slide for comparison of results. While the vertebrate nerve fibers were impregnated well with this technique, the chilopod tissue was not. The protargol method of Bodian (1936) was adopted and proved most effective. Several "protargol" products, however, were erratic. The Chroma¹⁰ silver protein, manufactured especially for use in Bodian staining, produced consistent success and was used throughout the present study.

The procedure outlined by Bodian was followed with slight modifications. Best results were always obtained with gold toning in 1.0-percent aqueous gold chloride without acetic acid. In the toning procedure, best contrast was given when slides were kept in 0.25-percent aqueous oxalic acid four times longer than in gold chloride. The time ratio, therefore, of gold chloride to oxalic acid was 1:4. Fifteen sec-

¹⁰ The registered trade mark for the West German products originally known as "Gruebler" stains.

onds in gold chloride and one minute in oxalic acid produced optimum results. Cresyl violet (0.25-percent aqueous) was used as a counter-stain after toning for demonstrating the neuronal cytoplasm. The microtechnical schedules found most effective are given as follows:

Paraffin method.

- 1. Kill and fix in modified Bouin's no longer than 12 hours, no less than 8. Decapitate and remove antennae, tips of poison claws.
- 2. Wash in several changes of 50-percent ethanol for 1 hour.
- 3. Dehydrate in ethanol/n-butyl series, combined as follows:

<i>Ethanol</i>		<i>n-butyl</i>	
(a)	25 ml. of 50 percent	4 ml.	1½ hr.
(b)	20 ml. of 70 percent	6 ml.	1 hr.
(c)	17 ml. of 80 percent	9 ml.	2 hrs.
(d)	11 ml. of 95 percent	14 ml.	2½ hrs.
(e)	6 ml. of 95 percent	19 ml.	6 hrs. (2 changes)
(f)	25 ml.	6 hrs. (no longer)

- 4. Complete dehydration and clearing in terpeneol, at least overnight. (Several days are not injurious.)
- 5. Infiltrate with paraffin-bayberry wax (9:1) in oven at 59°C. about five changes, or until the odor of lilac disappears, in the course of about 6 hours. (Material left longer does not harden appreciably.)
- 6. Block in paper boats, orient specimen quickly and cool; harden in cooled water.
- 7. Block is trimmed, squared after being affixed to wooden carrier, and sectioned at 10 micra.
- 8. Serial sections placed on clean slides, flooded with albumenized water, and placed on warming table (47°C.). Ribbons are stretched only if necessary.
- 9. Drain off excess fluid (much of the picric acid will be removed from tissue at this stage!); reorient ribbons; chill slide under dry ice for about a minute and blot gently, face down, on filter paper.
- 10. Continue drying on warming table; complete in desiccator for several hours before deparaffinizing.
- 11. To eliminate section loss, place slides in 0.1-percent celloidin in ether-alcohol (1:1) for 5 minutes after the second alcohol rinse in the deparaffinizing series.
- 12. Remove slides from celloidin solution, drain, and dry in air no longer than 1 minute; continue hydration as usual, omitting 95 percent alcohol.

Hansen's iron trioxymatein.

1. Steps 1 to 12, above.
2. Hansen's hematein, 3 minutes.
3. Wash in water, 10 minutes.
4. Aqueous picrofuchsin (10-percent acid fuchsin, aqueous: picric acid, saturated aqueous: distilled water (23:77:77)—no longer than 10 seconds.
5. Dehydrate rapidly, clear in xylol, and mount.

Silver impregnation procedure (Bodian's, modified).

Precautions: *All glassware must be scrupulously clean.* (Soak all glassware overnight in detergent, rinse in distilled water just before use.) *Use only chloride-free distilled water.* (Drop small crystal of AgNO_3 in sample of water. If precipitate forms, water is unfit for use.) *Use bone or plastic forceps only.* (Avoid use of any metal instruments or containers whatsoever.)

1. Steps 1 to 12 above.
2. Hydrate slides in at least four changes of distilled water for about $\frac{1}{2}$ hour.
3. Place slides in 1.0-percent silver protein solution, prepared as follows:
 - (a) Into 100 ml. of distilled water, place about 15 grams of metallic copper, which has been thoroughly washed in 70-percent alcohol (10 changes) and in distilled water (12 changes); and spread evenly on bottom of staining dish.
 - (b) Sprinkle 1 gm. of "silver protein, strong, highest purity for Bodian staining"¹¹ onto surface of water. (Do not stir while powder is on surface; let it dissolve without agitation.)
 - (c) Place slides gently into staining dish, cover and place in total darkness in incubator (37°C.) for 19 hours.
4. Remove staining dish from incubator, wash slides quickly in distilled water, rubbing debris from slides with finger.
5. Develop in the following reducing solution, made up fresh immediately before use, for 10 minutes:

¹¹ Catalogue No. M 773 p.

Hydroquinone	1.0 gm.
Sodium sulfite	5.0 gm.
Distilled water	100.0 ml.

6. Rinse slides (2-4 changes) in distilled water several minutes.
7. Gold tone immediately as follows:

(a) 1.0-percent gold chloride (*without* acetic acid), 15 seconds.

(b) Rinse briefly in distilled water, several dips.

(c) 0.25-percent oxalic acid, 60 seconds.

(d) Rinse in distilled water, about 30 seconds.

(e) 5-percent thiosulfate, 5 minutes.

(The gold chloride may be used repeatedly for about 100 slides; the oxalic acid and sodium thio-sulfate solutions should be made up fresh before use.)

8. Wash thoroughly in at least 12 changes of distilled water over a period of 1 hour.
9. Counterstain in 0.25-percent aqueous cresyl violet (Coleman and Bell Co.) for 6 minutes at 57°C. (Just before use add 15 ml. of 10-percent acetic acid to every 90 ml. of solution, heat gently and filter.)
10. Rinse in several changes of distilled water, dehydrate rapidly, clear in xylol, and mount.

RECONSTRUCTION TECHNIQUES

During the preparation of the microscopic material care was taken to avoid distortion of the internal structures. Efforts were made to orient the tissue blocks so that nearly perfect transverse, longitudinal, and horizontal sections were obtained. A dissecting microscope was often employed to orient the centipede heads in melted paraffin, since the cephalic capsule is about 1 mm. in length.

Photography of the stained sections greatly facilitated a study of each serial section and aided in the interpretation of relationships. All photographs were taken with a single lens reflex, 35-mm. Exakta camera and a compound microscope with apochromatic objectives. An illuminator with a ribbon filament, 6-volt tungsten lamp was employed. A green filter was used to increase contrast in the silver preparations. Panatomic-X film developed in FR X-22 was used, and enlargements were printed on F-4 Kodabromide paper developed in Kodak Dektol (1:2).

A number of adjacent photographed sections seen at a glance could be evaluated and examined without the distractions accompanying mechanical manipulation of the microscope. The finer details were, of course, checked and filled in from a direct observation of the microscopic preparations under the microscope. A stage micrometer, photographed at the same time and under the same conditions as the sections, afforded a method of accurate measurement, regardless of the enlargement factor. Occasionally tracings were made directly from the photographic enlargements using transillumination. Rapid sketches could be made with little effort and provided handy work sheets of structure outline. The photographic negatives furnished a permanent record of the series, and additional prints could be made when necessary.

Graphical reconstructions were also made directly from the microscopic material. By means of a microprojection apparatus, the dorsal, ventral, and sagittal views of the brain of *bipuncticeps* were thus constructed (figs. 1, 2, 3). With the aid of a stage micrometer, the apparatus was adjusted so that the diameter of the sections corresponded to the known thickness (10 micra) of the sections. Each division on the graph paper used (10 divisions to the linear inch) was made equivalent to 10 micra. Equal magnification of each section, the most important condition for accurate reconstruction, was thus insured. The reconstruction procedure was as follows: The image of a section was projected onto the graph paper. Pencil dots marked the limits of the anatomical entities which were to be reconstructed. The adjacent section was then brought into position, and dots were made on the next line of the graph paper. Additional sections were plotted until the entity being reconstructed was completely delimited. The dots were then connected by continuous lines, and the resulting outline was shaded for perspective effects in accordance with the observed contours in the microscopic sections. The bilateral symmetry of the brain exhibited in the transverse sections facilitated the selection of a reference point in each section. Alignment of reference points on a center guideline drawn on the graph paper insured accurate reconstruction. Only one aspect, obviously, can be reconstructed at a time.

IV. OBSERVATIONS

GROSS ANATOMY OF THE CEPHALIC NERVOUS SYSTEM

The cephalic nervous system of *bipuncticeps* is a small mass divided into an anterior supraesophageal and a posterior subesophageal

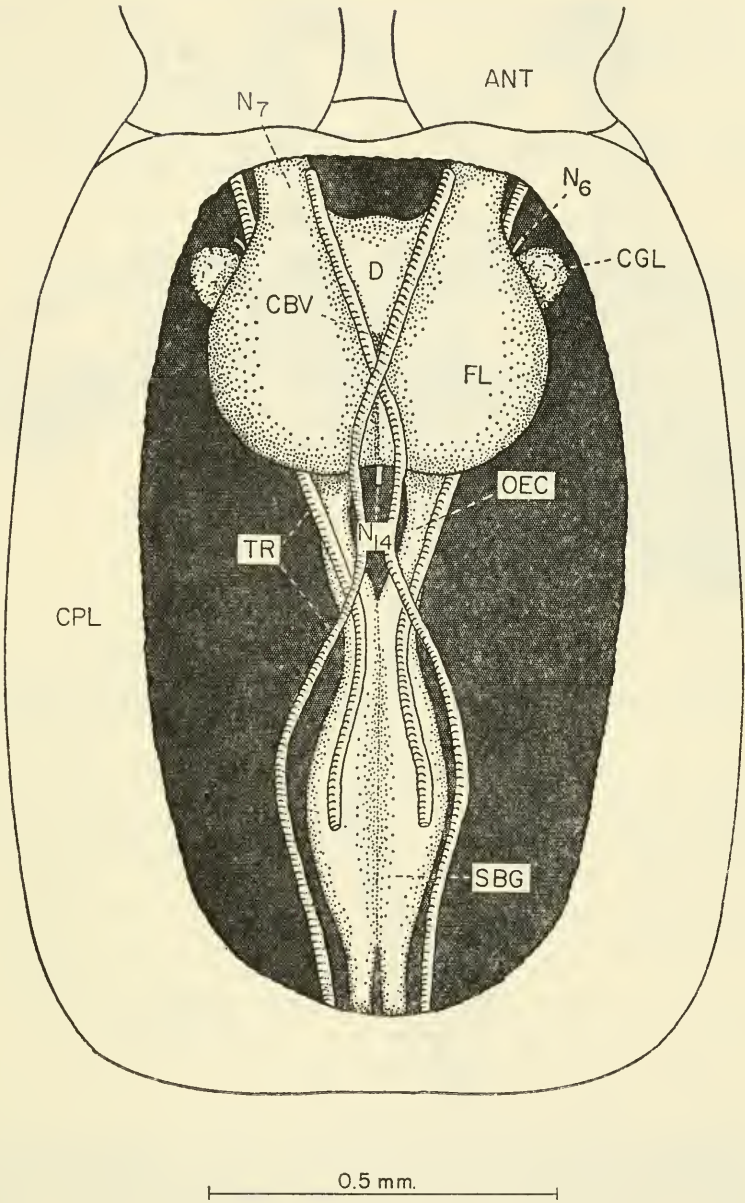


FIG. 1.—*Arenophilus bipuncticeps* (Wood), dorsal view of the head with part of the cephalic plate removed showing the cephalic nervous system. Note the position of the cerebral glands (CGL) and the cerebral haemolymph vessel (CBV). The latter is indicated by shading as emerging anterior to the crossed tracheae (TR), which served as reference points in the reconstruction procedure. (Graphically reconstructed from transverse serial sections.)

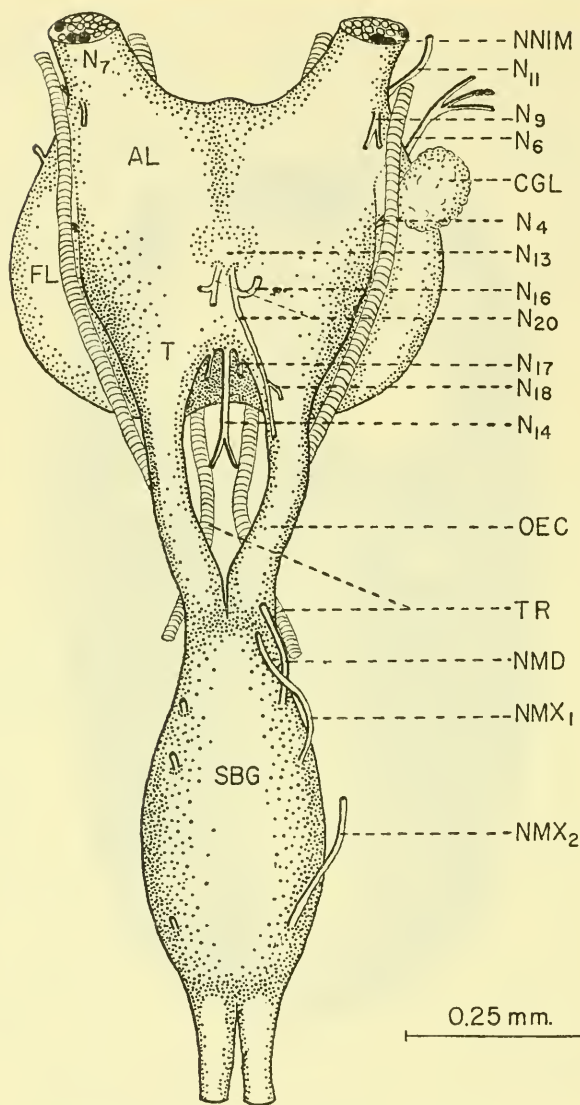


FIG. 2.—*Arenophilus bipuncticeps* (Wood), ventral view of the cephalic nervous system. The majority of cephalic nerves emerge from the brain and subesophageal ganglion ventrally. The three nerve fiber bundles in N₇ represented in section innervate the intrinsic antennary musculature (NNIM). See also plate 1, inset, and text for explanation. (Graphically reconstructed from transverse serial sections.)

ganglion. Cordlike circumesophageal connectives join the two ganglia, and both ganglia are located within the cephalic capsule (fig. 1). The

posterior ganglion is more ventrally situated than the anterior one. The esophagus passes between them and is bounded laterally by the circumesophageal connectives, which run in an anterodorsal-postero-ventral direction (fig. 3).

Viewed from the dorsal aspect the supraesophageal ganglion is relatively simple and almost circular. Transversely it is slightly wider

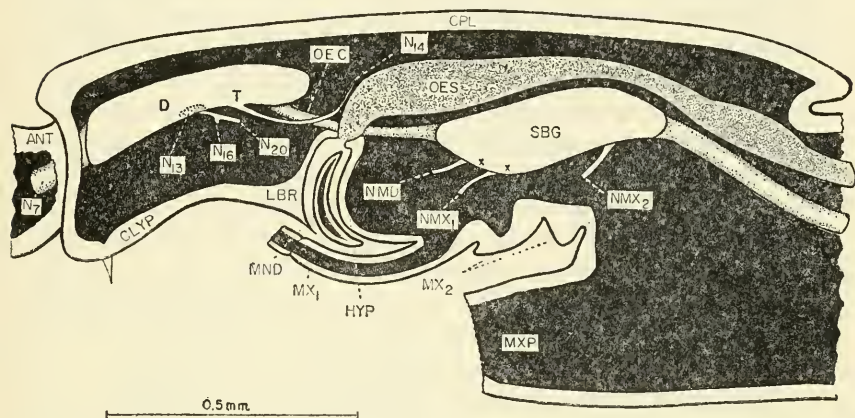


FIG. 3.—*Arenophilus bipuncticeps* (Wood), sagittal view of the head, showing the cephalic neural mass in relation to the exoskeletal structures and the esophagus (OES). The position of the two pairs of giant cells located in the subesophageal ganglion (SBG) is indicated by x's.

than it is long by a ratio of 9:7. The lateral and posterior borders are rounded in a smooth arc. The antennal nerves emerge anteriorly and are more widely separated than the posterior circumesophageal connectives. In the median plane a depression is seen anterior to the crossed dorsal tracheae (fig. 1). This is the exit of a canalicular structure, the "cerebral artery," which courses in an oblique postero-ventral direction (see fig. 5, B, and pls. 3 and 4).

The most striking feature on the ventral surface of the supraesophageal ganglion is a pair of circumesophageal connectives. These are continuous with the tritocerebrum which is poorly developed (fig. 2). The cerebral gland is laterally situated and projects beyond the lateral margin of the frontal lobe. A small nerve (N_4) innervates this gland (fig. 2). A larger nerve (N_6) emerges from the frontal lobe adjacent to the cranial border of the gland. The median recurrent nerve (N_{14}) emerges between the tritocerebral lobes and is closely associated with several other small nerves. These are described in the following section.

The subesophageal ganglion is an elongate mass located ventral to

the esophagus and overlying the roots of the mouth parts (fig. 3). The anterior margin of this ganglion is continuous with the circum-esophageal connectives. It is located at a point where imaginary transverse and sagittal midlines intersect on the dorsum of the cephalic plate (fig. 1). Nerves innervating the mandibles and maxillae emerge lateroventrally (fig. 2).

It is conventional (following the terminology of Viallanes, 1887) to divide the supraesophageal ganglion into three portions: protocerebrum, deutocerebrum, and tritocerebrum. Since these neuromeres are fused into a single mass in the brain of *bipuncticeps*, it is impossible to delimit their extent in whole mounts. The protocerebrum is poorly developed as contrasted with the brains of higher chilopods. In centipedes with well-developed eyes, i.e., the Scutigermorpha and some of the Lithobiomorpha, this region is large and distinctly delimited from the underlying deutocerebrum and tritocerebrum (fig. 4, A and B). A typical arthropod protocerebrum, however, is not present in the Geophilomorpha (fig. 4, D). It is represented only by the frontal lobes. The term "protocerebrum," nevertheless, will be employed to refer to the posterodorsal portion of the brain.

The deutocerebrum constitutes the major bulk of the brain of *bipuncticeps*. The two antennary lobes are distinctly separated in the brains of the other orders of centipedes (fig. 4, A, B, C) but in the geophilomorphs are fused at the midline (fig. 4, D). The deutocerebrum is mainly sensory and associational in function, as indicated by its connection with the antennae, but several motor nerves to the antennal musculature emerge from this region.

The poorly developed tritocerebral lobes begin as a fused central mass anteriorly but diverge at their posterior extensions as continuations of the circumesophageal connectives. The median recurrent nerve emerges between these two pyriform lobes and is flanked on either side by two smaller nerves which innervate the labrum (fig. 2, N₁₄). No free tritocerebral commissure was observed in this species.

CEPHALIC NERVES

The sites where the cephalic nerves emerge from the central neural mass were observed, but it was not always possible to trace the fibers to their terminations. The delicacy of the fibers, the thickness of the sections, and the varying degree of staining intensity of the surrounding tissue obscure the terminal endings. They seem to end in more than one structure. In a coordination center as complex as the cephalic nervous system this is not surprising. Rather than attempt

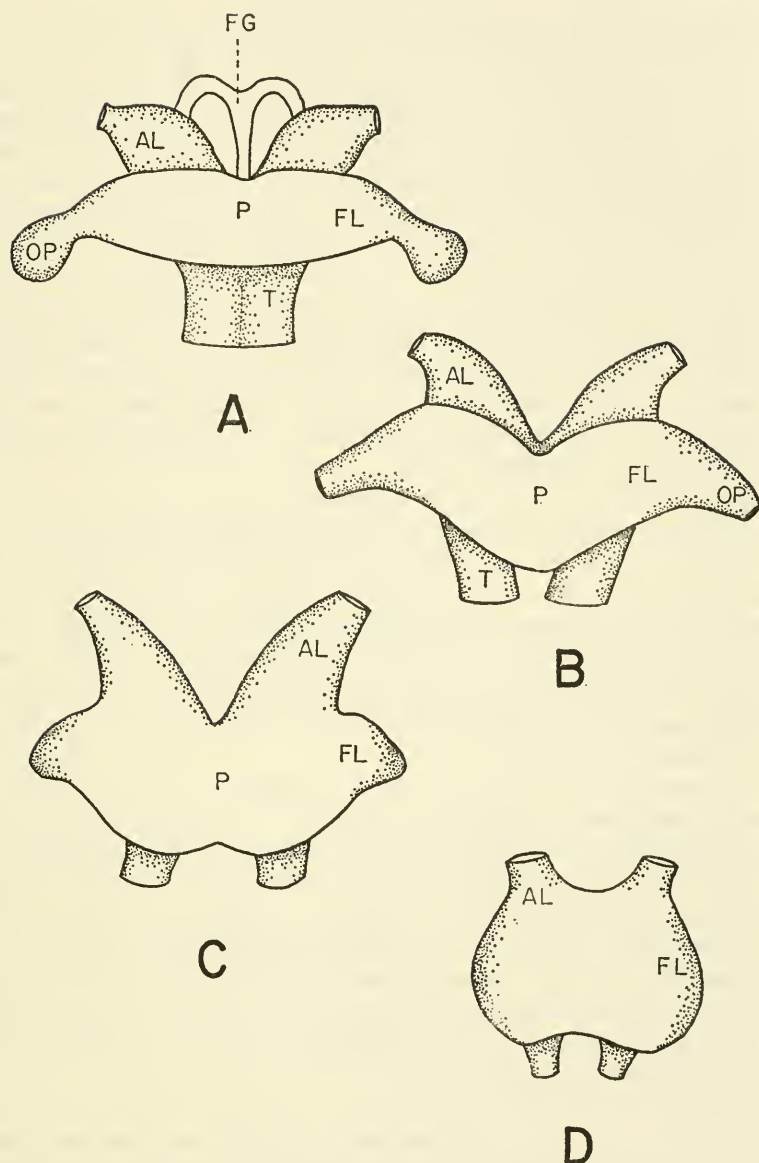


FIG. 4.—Schematic illustration, dorsal aspects, of the brains representative of the four orders of the class Chilopoda. A, The scutigermorph brain. The optic lobes (OP) and the frontal ganglion (FG) are well developed. B, The lithobiomorph brain. C, The scolopendromorph brain. D, The brain of *Arenophilus bipuncticeps* (Wood), representative of the geophilomorph. The protocerebrum is represented only by the frontal lobes (FL). (A, B, C, modified, after Fahlander, 1938.)

to develop a new terminology for the cephalic nerves of *bipuncticeps*, the numerical designations of Fahlander (1938) are used.

1. *Nerves of the protocerebrum*.—The nerve to the cerebral gland, N_4 , is present in *bipuncticeps*. This nerve emerges from the ventral surface of the brain as a minute filament. It is concealed by a trachea and a haemolymph vessel which are associated with the cerebral gland (fig. 2, and pl. 2, fig. 2.) The cells of origin of this nerve are located in the dorsal cortex of the frontal lobe. According to Scharrer (1941) and Gabe (1952), these cells are neurosecretory in other genera. The cytoplasm contains round granules which have a marked affinity for the acid dyes; acid fuchsin stains these granules a deep red (Gabe, 1952). In *bipuncticeps*, however, these cells show no such granules when stained with picric acid and acid fuchsin. Some pink granules were demonstrated in the tissue of the cerebral gland but not in the neuronal cytoplasm.

Arenophilus bipuncticeps is devoid of eyes and the Organ of Tömösvary. The optic nerve (N_1) and the nerve to the Organ of Tömösvary (N_3) are, therefore, absent. A small sensory nerve (N_2) to the dorsal integument of the cephalic plate, which was described by Fahlander (1938) in the Scutigeromorpha and Lithobiomorpha, was not observed. A nerve, called *nerf viscéral pair* by Saint Remy (1887) and reported to be deutocerebral in *Necrophloeophagus longicornis*, was not demonstrated in the present study and did not appear in Fahlander's material.

A sensory nerve enters the lateral portion of the frontal lobe and will be considered tentatively as protocerebral until its homology can be established. The fibers originate from the neurons peripherally situated in the lateral clypeus. Two or three distinct branches merge into a single nerve which enters the central neural mass (fig. 2, N_6). In the scutigeromorph this nerve enters the brain dorsomedially at a groove dividing the protocerebrum from the deutocerebrum. In lithobiomorphs and scolopendromorphs, it enters the frontal lobe proximal to the optic nerves. Fahlander, nevertheless, classified N_6 as a deutocerebral nerve.

2. *Nerves of the deutocerebrum*.—The largest cephalic nerve in *bipuncticeps* is N_7 , the antennal nerve. At its base there are from 15 to 18 bundles of fibers separated from one another by connective tissue (fig. 2). Three of these bundles may be traced to a group of neurons located in the ventromedial portion of the antennal lobes about 60 micra posterior to the anterior limit of the brain (pl. 2, fig. 2). Two of these fiber bundles are ventral in position, and one is lateral (pl. 1, inset). Since the distal articles of the antennae were

removed to facilitate infiltration, the fibers were not traced beyond the proximal articles. The fibers are probably motor since they are noticeably thicker and more heavily stained than those of the adjacent bundles, and they seem to originate from the nucleus which also gives origin to the fibers of N_9 . Thus they probably innervate the intrinsic antennary musculature. The remaining bundles of fibers in N_7 stain less intensely and are undoubtedly sensory to the antennae.

Two nerves, N_9 and N_{11} , innervate the extrinsic musculature of the antennae (fig. 2). This musculature is divided into a ventral and dorsal group which insert on the proximal articles of the antennae. The muscles originate on the cephalic plate and the tentorium. The ventral antennary muscles are innervated by N_9 which emerges from the ventrolateral surface of the brain medial to the large trachea (fig. 2) and about 60 micra posterior to the anterior limit of the brain. The nerve sends fibers anteriorly to terminate in finer branches in the ventral antennary musculature. The nucleus of origin of N_9 is adjacent to the group of neurons which are associated with the intrinsic antennary motor nerve (pl. 2, fig. 2).

In *bipuncticeps*, only one nerve, N_{11} innervates the dorsal musculature (fig. 2). It emerges from the lateral surface of the antennal lobes. N_{10} , which is a branch of N_{11} in *Strigamia hirsutipes* (see Fahlander, 1938, p. 89), was not observed. The fibers of N_{11} do not continue into the antennae with fibers of N_7 but are clothed in their own neurilemma.

3. *Nerves of the tritocerebrum.*—The tritocerebral lobes and the stomatogastric bridge are continuous with the antennal lobes anteriorly and the circumesophageal connectives posteriorly in *bipuncticeps*. The only vestige of an unpaired frontal ganglion is a mass of fibers and a few cells ventrally situated. The slight bulge which this structure makes on the ventral surface is likely to be overlooked in a gross dissection, since it is only about 50 micra in extent (fig. 2, N_{13} , pl. 3, fig. 3, STG). The stomatogastric bridge is formed from the frontal ganglion and the frontal connectives. The stomatogastric bridge represents the first anterior fibrous interconnection between the two sides of the brain. It occurs about 190 micra posterior to the anterior limit of the supraesophageal ganglion.

Fibers which contribute to the formation of N_{20} originate in the neuropile of the tritocerebrum. After this nerve emerges from the ganglionic mass, it gives rise to a branch (N_{16}) (fig. 2). This branch innervates a longitudinal group of muscles located on either side of the clypeal midline. Another branch (N_{18}) arising caudal to the first branch, proceeds laterally to terminate on each side of the anterior

portion of the oral opening. A nerve to the hypopharynx (N_{19}) described in *S. hirsutipes* by Fahlander was not observed in *bipuncticeps*. Neither did N_{20} exchange fibers with its fellow of the opposite side. A free tritocerebral commissure, therefore, does not appear in *bipuncticeps*.

The unpaired recurrent nerve N_{14} , emerges 50 micra caudal to the roots of N_{20} . The recurrent nerve is dorsal to and runs between the *levator pharyngis* muscles which insert on the pharynx (pl. 4, figs. 1-3). On each side of this nerve the labral nerve, N_{17} , is observed. These three nerves and a pair of tracheoles emerge simultaneously from the ventral surface and form a "sort of tuft." This expression was used by Saint Remy (1887) in describing the same site in *Necrophloeophagus longicornis*. The recurrent nerve continues caudad for about 100 micra and bends sharply dorsad onto the esophagus (fig. 3). The nerve then branches into two nerves on the dorsal surface of the esophagus. They were not traced beyond the point of bifurcation.

4. *Nerves of the subesophageal ganglion.*—Three pairs of nerves emerge from the lateroventral aspect of the subesophageal ganglion. The mandibular nerve (fig. 2, NMD) emerges anteriorly. It is closely followed by the nerve to the first maxilla (NMX_1). The nerve to the second maxilla (NMX_2) emerges from the ganglion posteriorly. In *bipuncticeps* the nerves to the first and to the second maxillae are widely separated. The three nerves are sensory to the receptors and motor to the intrinsic muscles of the mouth parts.

HISTOLOGY OF THE CEPHALIC NERVOUS SYSTEM

The histology of the nervous system of *bipuncticeps* is typically arthropod in appearance. The ganglia and the nerves outside of the ganglia are covered with a connective tissue sheath called neurilemma. The neurilemma of the ganglia was previously thought to have the same construction as that enveloping the peripheral nerves and connectives. Recent studies, however, reveal that the nerves have a connective tissue layer and a Schwann cell layer, while the ganglia have a thicker connective tissue layer, a perilemmal cellular layer, and neuroglial cells (Hess, 1958).

1. *Neurilemma and neuroglia.*—The neurilemma is composed of an outer homogeneous covering called the neural lamella, and an inner cellular layer called the perilemma. This neurilemma may vary in thickness within the same species. In *bipuncticeps* the ventral surface of the brain has a thicker neurilemma than the dorsal surface. It may vary from about 2 to 8 micra in thickness.

The neural lamella stains bright pink with picrofuchsin. There are no cells present in this homogeneous sheath. In sections which are distorted it is seen to consist of several laminae. The cells in the underlying layer are thought to produce the neural lamella.

The cells of the perilemma are differentiated in silver and cresyl violet preparations. At least three nuclear types are distinguishable on the basis of shape and staining properties (pl. 5, fig. 1). One type (*a*) of nucleus is almost spherical. It is almost opaque and the cell has very little cytoplasm. A second type (*c*) has an oval nucleus whose chromatin stains a bluish black and is heavily distributed throughout the nucleus. A third type (*b*) stains light pink. Its chromatin is aggregated along the nuclear membrane. A clump of chromatin, probably a nucleolus, is eccentrically placed against the nuclear membrane. The third type resembles one of the neuroglial cells which occur within the cortex and neuropile in that it stains pink and has similarly distributed chromatin. The cell types found in *bipuncticeps* are similar to those described in the thoracic ganglion of *Periplaneta* (Hess, 1958).

The neuroglial nuclei are smaller than those of the neurons and stain less intensely. Two types of "glial" cells can be differentiated on the basis of their nuclear properties. Both nuclei are ellipsoidal (3×5 micra) but occasionally assume different shapes, which may be the effect of fixation or position in the ganglia. They are generally kidney shaped in the neuropile. Dark and light staining cells are present in silver and cresyl violet preparations. The dark cells have a great abundance of chromatin which is distributed in clumps and strands throughout the nucleus and which stains black. The light cells have less chromatin. This is aggregated near the nuclear membrane and stains pink. Eccentric nucleoli less than a micron in diameter are present. The two types of glial cells are represented in plate 5, figure 2.

2 *Cellular cortex*.—The brain of *bipuncticeps* consists of an outer cellular cortex and an inner fibrous core. The cortex contains the cell bodies of the neural elements, and the fibrous core, also called the neuropile, neurospongium, or, by some European authors, "punktsubstanz," contains the cell processes or nerve fibers. Routine histological stains, such as haematoxylin and eosin, trichrome stains, etc., do not reveal the precise fibrous nature of the neuropile; special silver-staining techniques are required. The cortex and neuropile exhibit a precise bilateral symmetry. Even the number and location of the nuclei reflect this symmetry.

Sensory neurons have not been demonstrated in the ganglia of

arthropods. They are located near the receptors in the epidermis. The cell bodies located in the cephalic nervous system of *bipuncticeps* fall into three categories: motor neurons, internuncial, or associational neurons, and neuroglial (supporting) cells.

The motor neurons are typically pyriform, unipolar nerve cells which are rich in cytoplasm. A moderate amount of chromatin is present in the nucleus. The single "stalk" or cell process usually projects radially inward into the neuropile. The main process gives off a collateral in the neuropile but continues uninterrupted to the effector which it innervates. The collateral makes numerous connections with the other elements in the neuropile and cortex, principally with the associational components.

The majority of cells found in the cortex of the brain are association neurons. They are usually smaller than the motor neurons, and their spherical nuclei are heavily stained in silver preparations. In certain areas of the brain, particularly in the posterior cortex, these cells are so crowded together that their nuclear membranes appear to be touching. Very little cytoplasm surrounding a dark spherical nucleus usually identifies the cell body as an associational neuron.

Typical neurosecretory neurons were not observed in the frontal lobes or in any other part of the supraesophageal ganglion with the stains employed. In the subesophageal ganglion, however, four large cells were discovered which may have neuroglandular significance. The main center of neurosecretory activity has been found to be located in this ganglion in a number of arthropods (Scharrer, 1941). In *bipuncticeps* these large cells occur 70 to 100 micra posterior to the anterior limit of this ganglion. They are ventrally situated on either side of the midsagittal plane (fig. 3 indicated by x's.).

The cells are pyriform and unipolar and have a large amount of cytoplasm. The single stalk is directed dorsad and enters the neuropile. Their dimensions are approximately 12×20 micra. The nucleus is ellipsoidal and measures 5.7×6.9 micra. A dark, spherical nucleolus about 1.5 micra in diameter is present and is eccentric in position (pl. 5, fig. 3). These cells are probably the largest found in the nervous system of *bipuncticeps* and are considered "giant cells."

In addition to the neuronal cells located in the cortex, neuroglial cells occur. These may be found in the neuropile as well as in the cortical layer. They have already been described.

An abundance of tracheoles and tracheal fibers penetrate the neural substance. These have been mentioned for two reasons: (1) They are easily mistaken for nerve fibers in some "unsuccessful" silver impregnations; (2) they are accompanied by elongate and flattened

cells (pl. 5, fig. 1) which may be confused with neuroglial or perilemmal elements. These cells adhere to the surface of the tracheoles and may be observed at the site where certain nerves (e.g., N_{14} and N_{17}) emerge from the central neural mass.

3. *The neuropile*.—The histology of the neuropile is more revealing in the present study than is that of the cortex. The three neuromeres of the brain of *bipuncticeps* are easily homologized with these entities as they are exhibited in other arthropods by a study of the neuropile. The limits and extent of the protocerebrum, deutocerebrum, and tritocerebrum are poorly outlined in gross dissections as they are extremely reduced. Silver impregnations reveal, however, that the medullary substance is arranged according to a definite pattern, and the apparent radical departure of the geophil brain from the typical arthropod plan is clarified.

The protocerebrum is identifiable by the presence of the "frontal lobes." These lobes are weak, lateral outbulgings of the neuropile (pls. 3 and 4). The deutocerebrum is represented by the antennal lobes situated anteriorly. These are two bilaterally symmetrical bodies which are separated by an area of cortical cells located in the midline for the major portion of their extent (pl. 2, fig. PI [AL]). Only a microscopical study reveals this separation. The deutocerebrum is ventral to the protocerebrum posteriorly and is continuous with the tritocerebrum and the circumesophageal connectives. Fibers interconnect each of these neuromeres and distinct fiber tracts are traceable.

In naming the fiber bundles in the brain of *bipuncticeps* we have attempted to recognize homologies with the entities previously described in other centipedes. Invention of a new terminology would be confusing and tends to overlook the significance of biological affinity. The names employed are subject to correction if additional information makes this necessary.

The fiber groups in the brain of *bipuncticeps* were carefully studied with the intention of determining probable interconnections and spatial interrelations before names were assigned. This appeared to be the only logical approach to the problem. If it be assumed that the supraesophageal ganglion of this centipede is homologous with that of *Thereuopoda*, whose tracts were studied by Fahlander, then some order can be found in the neuropile of the geophil brain.

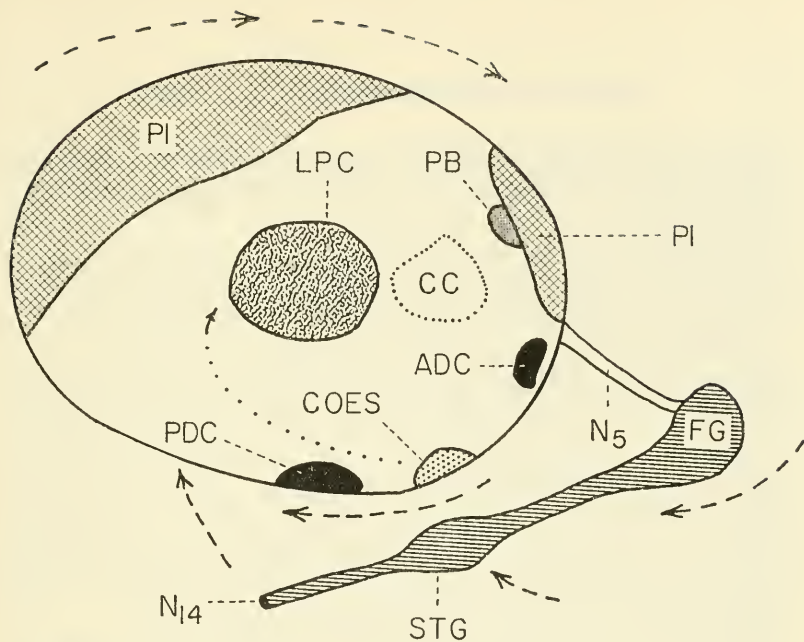
The head of the scutigeromorph is roughly globose, resembling in certain respects the head of an insect; the head of *bipuncticeps*, however, is extremely compressed dorsoventrally. If one imagines the ventral portion of the brain of the scutigeromorph to be shifted posteriorly and the dorsal portion anteriorly, and the relocated structures

flattened (fig. 5, A, indicated by broken arrows) the resulting brain would resemble that found in the geophil head capsule. The free frontal ganglion and the stomatogastric ganglion are now incorporated in the neural mass instead of having their own neurilemma. The antennal lobes are joined at the midline while still separated by a cellular cortex, and the protocerebrum is compressed. Figure 5, B represents a schematic sagittal section through the supraesophageal ganglion of *bipuncticeps*. Terms can now be assigned, tentatively, to the various glomerular elements in the brain of *bipuncticeps*.

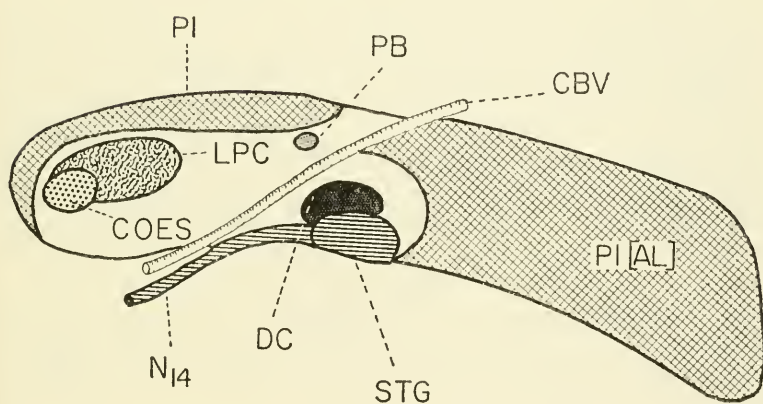
The deutocerebrum is considered first. About 60 micra posterior to the base of the antennal nerves, a marked indentation of the neuropile, approximately 40 micra in length, exists. This suggests the presence of a medial and a lateral lobe (pl. 2, fig. 3, Dl, Dm). Between these lobes courses a fibrous structure which is probably homologous to the "corpus lamellosum" (clm) found in the other three orders of chilopods. As the name suggests, this glomerulus consists of densely aggregated parallel fibers. This tract consists of fibers which run between the medial and lateral lobes in a dorsolateral-ventromedial direction. The tract bends abruptly caudad about 100 micra from the anterior margin of the brain. It continues into the circumesophageal connectives. It receives fibers from the cells of the "pars intercerebralis" (pl. 3, fig. 1). Whether the tract of the opposite side sends fibrous connections by way of the region of the stomatogastric bridge is not certain. The fibers lose optical individuality in this region and cannot be followed with precision.

A bundle of fibers in the lateral lobe of the deutocerebrum follows a path parallel to the tract just described. It assumes a position lateral to the corpus lamellosum in the circumesophageal connectives. These two pathways undoubtedly establish connections between the antennae and the subesophageal ganglion. Whether they are motor or sensory or both cannot be determined in the present study. The evidence that connections exist is indirect and is suggested by the manner in which this species "cleans" its antennae with its mouth parts.

In addition to a large glomerulus ventrally situated at the rostral limit of the antennal lobe (pl. 2, fig. 1, *glom*), two small adjacent dorsolateral glomeruli are present in the medial lobe of the deutocerebrum. These are most probably the "antennal glomeruli" described by other authors. In a brain of this size they may be easily overlooked. Saint Remy mentioned the presence of "glomerular concentrations" in *Necrophloeophagus longicornis* but gave little attention to their histology. The antennal glomeruli in *bipuncticeps* lack the scalloped appearance of the antennal glomeruli in the higher arthro-



A



B

FIG. 5.—Diagrammatic sagittal section through the brains of A, a scutigeromorph (modified, after Fahlander, p. 57, fig. 23), and B, *Arenophilus bipuncticeps* (Wood). Homologies are represented by the same shading patterns. The antennal lobes, separated in the scutigeromorph (see fig. 4, A), do not appear in section. The central complex (CC) is lacking in *bipuncticeps*. The anterior (ADC) and posterior (PDC) commissures of the deutocerebrum are not separate entities in *bipuncticeps* but represented as fused (DC). Note that the frontal ganglion and stomatogastric ganglion are separated from the central neural mass in A, and indicated only by STG in B. (See text for explanation of broken arrows.)

Pods and are not easily identified. In silver preparations the matrix of these entities is amorphous, but a few dark fibers are seen scattered throughout it.

It is generally accepted that this homogeneous ground substance is made of innumerable fine, branching, arborizing fibers interwoven and matted together, but . . . they are not visible as separate entities. (Power, 1946b, p. 488.)

Another tract associated with the glomeruli of *bipuncticeps* may be called the "olfactorio-globularis" tract. Hanström (1928) considered this to be one of the most primitive tracts in the arthropod brain having antecedents, perhaps, in the Annelida. Its presence may be expected, therefore, in the geophilomorph brain. Like so many fibers in our preparations, those associated with this tract are extremely difficult to follow. It is most probable, nevertheless, that some of the fibers cross to the opposite side by way of a small commissure located dorsoposteriorly in the protocerebrum (pl. 3, fig. 2, PB).

There are no structures in the cephalic nervous system of *bipuncticeps* which can be homologized with the "corpora pedunculata" or with the "central complex" of the scutigeromorph and higher forms. These components are well developed in the higher arthropods with compound eyes, especially the social insects (Kenyon, 1896; Thompson, 1913; Power, 1943) and are, in large part, fibrous entities. They are poorly developed in the Lithobiomorpha and Scolopendromorpha (Fahlander, 1938). In *bipuncticeps* the "pars intercerebralis" consists of a cellular cortex and occupies the greater extent of the midline between the frontal and antennal lobes. The first anterior continuity of the neuropile in the median plane occurs in the anterior half of the tritocerebrum. This however, has already been identified as the stomatogastric bridge. A diffuse array of fibers which probably represent a fusion of the anterior and posterior commissures of the deutocerebrum (fig. 5, DC=ADC+PDC) is dorsal to this bridge and slightly caudal. Fibers run, it appears, in every direction. It is highly improbable, therefore, that either of these represent vestiges (or Anlagen!) of the corpora pedunculata or central complex of the higher arthropods.

A commissure occurs between the frontal lobes about 40 micra caudal to the stomatogastric bridge. It is dorsal and posterior to the canalicular space containing the median cerebral vessel. This narrow file of fibers is considered to be the "protocerebral bridge" (pl. 3, fig. 2).

A large mass of commissural fibers is observed about 30 micra caudal to the protocerebral bridge. Its dimensions are enormous in contrast to the other commissures mentioned (pl. 4, figs. 1-3). Begin-

ning about 90 micra anterior to the caudal end of the brain this transverse file extends almost to the posterior boundary of the ganglion. Heavily stained fibers interconnect the frontal lobes, the deutocerebral lobes, and the bases of the tritocerebral lobes. Connections are also made between the circumesophageal connectives at their anterior end (pl. 4, fig. 2). This large commissure is obviously the most important association area in the brain of *bipuncticeps*. Although connections with fibers derived from the three neuromeres are made at every level, there is a pattern which can be resolved by resorting to the postulated shifting of commissures (fig. 5).

The majority of fibers which cross the large commissure in the anterior portion are derived from the lateral portion of the frontal lobes (pl. 4, fig. 1). This morphological observation identifies the anterior portion of the tract as the "large protocerebral commissure" of other authors. Fibers which are clearly derived from the deutocerebral region are seen farther caudally. These fibers arch dorsally above the cerebral vessel. Fibers from the dorsal bases of the tritocerebral lobes, where the circumesophageal connectives take origin, are located still more caudally. Arcuate fibers intercommunicate the tracts in the connectives. This has been named the "commissure of the circumesophageal connectives" (pl. 4, fig. 2, *COES*).

The position of the "commissure of the circumesophageal connectives" is the only radical displacement of commissural elements in the brain of *bipuncticeps*. The translocation of this commissure—from a position (in the scutigermorph brain) anterior and ventral to the "large protocerebral commissure" (fig. 5) to one posterior to it—is difficult to reconcile. The difficulty, however, is only spatial. The fiber interconnections which are observed in the neuropile warrant the homology.

V. DISCUSSION

THE GANGLIA

The geophilomorph has a simply organized cephalic nervous system and is the least complex of the chilopod brains. The spadelike cephalic capsule has resulted in a wide separation of the supraesophageal and subesophageal ganglia with a lengthening of the circumesophageal connectives. The connectives are longer than those found in the other chilopod orders. In the scutigermorphs and insects the two ganglia are practically one, and the esophagus courses through what appears to be a single neural mass; the connectives are short, if present at all as observable entities. In *bipuncticeps*, however, the connectives are long, thin, and cordlike. Its cephalic nervous system superficially

resembles that of the Annelida. This similarity to the annelid system was recognized about a century ago by at least two workers (Newport, 1843; Walter, 1863).

The protocerebrum is virtually lacking; only the frontal lobes exist. The absence of light receptors and of the Organ of Tömösvary results in a reduction of the size and number of neural components in this region of the brain. The deutocerebrum, on the other hand, is well developed. The majority of fibers associated with the deutocerebral lobes originate from the sensory neurons in the antennae and the associational neurons of the cortex. The tritocerebrum is extremely reduced and modified in structure, as compared with the other orders of centipedes. The frontal ganglion and its connectives and the stomatogastric ganglion in the Scutigermorpha are separated and clothed in their own neurilemma. In *bipuncticeps* these elements are incorporated into the central neural mass so as to be indiscernible. They are aggregated at the site of the "stomatogastric bridge."

THE CEPHALIC NERVES

The protocerebral nerve to the cerebral gland (N_4) is concerned with neuroglandular activity. Fahlander was the first to hint at the true nature of this nerve. It had been called "nerf de Tömösvary" (Saint Remy, 1887), "der Nerv der ursprünglich zweiten Antenne" (Haller, 1905, p. 199), and the "nerve of the frontal organ" by other authors. Holmgren (1916) followed its intraganglionic path using the methylene blue technique but considered it the "Nerv des Frontalorgans." The data given by Fahlander and the name he used, "Nerv zur Gehirndrüse," are most valid and appropriately indicate its neurosecretory nature, as supported by the work of Gabe (1952). In our material, moreover, the presence of a haemolymph vessel passing through the tissue of the cerebral gland supports the high probability that it has an endocrine function. Fahlander compared this gland with the corpora allata of insects and the X-organ of crustaceans. Gabe (1952) disagrees and claims that the histological data warrant comparison with the corpora cardiaca and the sinus gland.

Fahlander grouped N_6 , a nerve from the lateral clypeus, with the deutocerebral nerves in *Thereuopoda*, but expressed a doubt that it was. In the other orders, this nerve is clearly associated with the protocerebrum and emerges from the proximal end of the optic lobe. This nerve is considered to be protocerebral in *bipuncticeps*.

The descriptions of the motor antennal nerves of the deutocerebrum of *bipuncticeps* do not follow Fahlander's account of their arrangement in *Strigamia hirsutipes*. He did not distinguish between in-

trinsic and extrinsic antennal musculature. The motor antennal nerves in *bipuncticeps* originate from a nuclear group ventrally situated in the antennal lobes. Motor fibers were identified in N_7 and traced to the same nucleus of origin as the fibers of N_9 and N_{11} , the nerves to the extrinsic antennal musculature. Fahlander reported that N_{10} , a branch of N_{11} , innervated the dorsal musculature in *S. hirsutipes* and that N_{11} continued into the antennae with the fibers of N_7 . In *bipuncticeps* however, N_{10} is absent and N_{11} itself innervates the dorsal extrinsic musculature of the antennae. Fahlander may have mistaken the fibers of one of the intrinsic motor nerves for those of N_{11} .

No "free tritocerebral commissure" is present in *bipuncticeps*. Saint Remy (1887) was not able to demonstrate it in *Necrophloeophagus longicornis* and said that its absence is well explained by the concentration of the tritocerebral ganglion. Fahlander admitted that he did not find a continuity between N_{20} of one side and that of the opposite side but still did not "doubt that the Geophilomorpha concur in this respect with the other chilopod orders." His effort to homologize the four orders of centipedes hindered him from conceding that a free tritocerebral commissure, which he had demonstrated in the other three orders, could be absent in the geophilomorphs.

It is customary to consider a *dorsal* motor and a *ventral* sensory root in a typical arthropod ganglion (Wigglesworth, 1953). This arrangement is inverted, however, with reference to the antennal motor nerves in *bipuncticeps*. Their nuclei of origin are ventral in position. In the subesophageal ganglion efferent neurosecretory neurons are also ventral in position. Most of the neurons, in fact, are ventrally aggregated in this ganglion. Experimental studies of nerve degeneration and chromatolysis, as performed by Vowles (1955), would probably indicate that the ventral surface of the subesophageal ganglion is a motor area. It is hoped that this may be investigated in the future.

The nerves which innervate the mouth parts of *bipuncticeps* emerge from the subesophageal ganglion, and in general, agree with the arrangement in *Strigamia hirsutipes*. The nerves to the mandible, first, and second maxillae, in *S. hirsutipes*, are equidistant from one another; in *bipuncticeps* the nerves to the mandible and first maxilla are anteriorly located while the nerve to the second maxilla is considerably more posterior in position. This is probably related to the fact that the ganglion of *S. hirsutipes* is spherical while that of *bipuncticeps* is elongate. The entire cephalic capsule of *bipuncticeps* is, in fact, longer than that of *S. hirsutipes*.

CELL TYPES

The types of nerve cell bodies observed in *bipuncticeps* resemble those of other arthropods with reference to relative size and shape. The motor, associational, and neuroglial nuclei may be differentiated on the basis of size and the nuclear properties already described. The cells described by Gabe (1952) were not observed in the frontal cortex, probably because specific stains for secretory granules were not employed. In a preparation in which a contaminated metachromatic dye was accidentally used, however, some evidence of neurosecretory activity was seen, not in the cells of origin but in the tissue of the cerebral gland. This requires further investigation.

NERVE TRACTS

The difference between the glomerular entities in the neuropile of *bipuncticeps* and those of other centipedes, particularly the Scutigermorpha, are probably due to phylogenetic modifications. Homologies undoubtedly exist. The scutigeromorph head is domed and resembles that of an insect, in that the antennae are dorsally placed and the mouth is pushed forward so that the labrum and clypeus form the front boundary of the head. In *bipuncticeps* the head is flattened dorsoventrally so that the mouth, clypeus, and labrum are ventrally located. The antennae are rostrally situated. The general configuration of the cephalic capsules accounts for many of the differences between the geophilomorph and scutigeromorph brains. The positions of the antennal lobes and tritocerebral components in the brain of *bipuncticeps* become intelligible. The reduction of the protocerebrum is related to the absence of eyes and the Organs of Tömösvary, and the absence of the corpora pedunculata and of the central complex follows logically. The other tracts may be homologized on the assumption that the shapes of the heads are correlated with a spatial displacement of fibers.

THE FAHLANDER-FERRIS CONTROVERSY

Fahlander's contribution to chilopod neuroanatomy has proved a most reliable source in this study, but a single statement found in Ferris (1953) is sufficient to jeopardize the value of the former's research. "It is not a criticism of the author of this work [Fahlander, 1938] to say that as far as the nervous system is concerned the work fails." (Ferris, 1953, p. 12.)

After World War II, G. F. Ferris began a study of the comparative

morphology of the Annulata (=annelid-arthropod complex). In a paper entitled "The Contradictions of the Insect Head," he stated:

The processes of change which have produced the millions of species, living and dead, that belong and have belonged to the super-phylum Annulata have left the central nervous system basically unaltered. A system that must have been established in the Precambrian has come down to the present time so little altered that a point-by-point correspondence may be shown to exist on even some of the smaller details throughout the vast group that has been derived from Annelid-like ancestors.

This is the fundamental significance of the facts that will be presented. (Ferris, 1947, p. 64.)

This concept is the starting point from which Henry (1947, 1948) undertook the study of the "Nervous System and the Segmentation in the Annulata," which appeared under that title in five articles. She considered the problem of segmental homology in the oligochaete annelids up through the insects. Included in her work is a brief treatment of a large gosibiid centipede, *Pseudolithobius megaloporus* (Stuxberg). She interpreted the segmentation of the chilopod head and the disposition of the cephalic nerves in the light of her investigations on the nervous systems of the Polychaeta, Onychophora, and Crustacea.

Applegarth (1952) continued the program with a study of the cephalic musculature and innervation of the same lithobiomorph. He interpreted his findings in accord with the principles outlined by Ferris (1948) and the conclusions given by Henry (1948). The bibliographies of these workers did not include Fahlander (1938) until Applegarth (1952) had completed his doctoral dissertation. In a supplementary note, he wrote:

it appears that Fahlander's paper contains numerous errors, small in themselves, but of such a nature as to preclude the development of any understanding of the relation of the muscles of the head region to the segmentation of that area. (P. 143.)

Ferris (1953) summed up the work he had initiated and defended his morphological principles. He concluded a section devoted to the Chilopoda with a bitter criticism of Fahlander's efforts. Comparison of the various areas of controversy revealed the following discrepancies:

(1) Fahlander described a short, thin, motor nerve (n_8) which innervates a part of the *levator pharyngis* muscle and which arises from the deutocerebrum. Ferris, on the other hand, said that no such nerve existed in his material. A nerve corresponding in position occurs but goes to the integument between the bases of the antennae.

Ferris failed to emphasize that Fahlander was describing the nerve as it occurs in the scutigeromorph *Thereuopoda*. Fahlander made no mention of this nerve's occurrence in the other species he studied—either in the text or in the figures.

(2) Fahlander described a nerve (n_5) which originates between the protocerebrum and deutocerebrum whose destination is the frontal ganglion. Ferris denied its existence: "No such nerve appears in our material. No such nerve should be present. If the generalizations previously offered are valid no such nerve can be present." (P. 12.) Fahlander was still, however, referring to the organization of the brain of *Thereuopoda*. The nerve in question is conspicuously absent in the other three representatives he described and illustrated.

(3) Fahlander described still another nerve (N_{17}):

Die Labralnerven gehen vom Tritocerebrum gleichzeitig mit den Frontalkonnektiven ab und bilden einen Plexus praefrontalis ganz kranial in Kopf. Von dort gehen Nerven für die clypeale Muskulatur sowie die sensorischen Nerven des Labrum aus. (P. 81.)

Ferris criticized him principally on the basis of a definition of muscle origin and insertion which first appeared in Applegarth (1952, p. 132). Fahlander made no reference to origin or insertion in the clypeal musculature. It is clear, furthermore, from his own words and from the German idiom, that he was referring primarily to the *plexus praefrontalis* and not to a direct branch of the labral nerve as Ferris described it. On the contrary, Fahlander wrote, concerning *Lithobius*:

Der Frontalnerv (n_{16}), welcher unpaar ist, aber eine doppelte Wurzel besitzt, verläuft in kranialdorsaler Richtung und innerviert die Clypeusmuskulatur. Er hat *keinerlei Verbindung mit den Labralnerven* (n_{17}), die vom kaudalen Teil der Brücke abgehen und *sensorisch sind*. Ausser zum Labrum schicken die Labralnerven Äste zur lateralen Partie des Clypeus. (P. 85.) (*Italics mine.* M.A.L.)

Fahlander is beyond reproof on this point of Ferris's criticism.

(4) Fahlander described a free tritocerebral commissure in *Lithobius* (p. 86 and fig. 29). It is represented as a dorsal and ventral doublet having connections with two other nerves. Ferris, however, denied that such a commissure existed in his material. He suggested that paired stomodaeal nerves innervating the esophagus may have been mistaken for a free tritocerebral commissure. Fahlander was aware that this structure was a subject of controversy and Ferris admitted that it may be present in some species and not in others as had been shown in the insects. Both authors could be correct since they concerned themselves with different species of lithobiomorphs.

(5) Fahlander claimed that nerves proceeding from the commis-

sure in question innervate the hypopharynx. Ferris disagreed repeatedly throughout his article with Fahlander's description of hypopharyngeal innervation but added: "There are present a pair of nerves . . . corresponding in position to Fahlander's n_{20} but which innervate the muscles of the hypopharynx with a branch proceeding laterally of the mouth opening." (P. 12.) Fahlander's n_{20} is the tritocerebral commissure!

It at once becomes clear to one who has studied both articles that the interpretation given by Ferris to Fahlander's descriptions do not seem to be accurate. On the contrary, the reliability of Fahlander's work has been enhanced by the study of the points of disagreement uncovered by his antagonist.

CONCLUDING COMMENTS

The results of this paper do not allow broad speculation on the problem of chilopod evolution; general conclusions are impossible without considering all the morphological features as a whole. This research was initiated on the supposition that the nervous system of the Geophilomorpha might furnish evidence conducive to a solution of the problem of their disputed position on the chilopod tree. Some authors have considered the scutigeromorph as primitive and the geophilomorph as degenerative; others have looked upon the modern centipedes as offshoots of a geophiline stock.

In the course of the study of the nervous system of *bipuncticeps*, the relevant literature was consulted and it was found that in each order of the class there is an admixture of features, some presumably conservative, others theoretically highly derivative. The presence of compound eyes in the scutigeromorph, the shape of the head capsule and position of the antennae, the peculiar scape organ of the antennae—found nowhere else among the centipedes—set this order apart from the rest of the Chilopoda and closer to the higher insects. The geophilomorph, on the other hand, with its absence of eyes and of the Organs of Tömösvary, its homomeral condition and intraspecific variation of the number of segments, manifests a simplicity only vaguely hinted at in the Scolopendromorpha. It is indeed a difficult task to answer the question: Which of the present-day chilopod orders has the closest affinity to the primitive condition of the hypothetical "Ur-Chilopoda"?

Homomerism and high and variable number of tergites have been considered primitive characteristics; the Geophilomorpha alone approximate this condition. Heteromerism with a low and fixed number of tergites has also been called primitive; the other three orders mani-

fest these characteristics. The compound faceted eye is regarded as highly specialized by most entomologists, but some regard its presence in the scutigeromorph as primitive. The absence of a visual apparatus is degenerative or primitive depending on the taxonomic scheme one favors. Anamorphosis and epimorphosis are simultaneously the primitive postembryonic state!

Are the simplicity of the geophil brain and the absence of photo-conductor elements in the neuropile conservative or specialized? Fahlander's aversion to more than one parallel evolution seems to be the prime reason for his refusal to admit that the geophilomorph may represent the primitive stock of the Chilopoda. Although his argumentation is sound, it rests on an undemonstrated "principle of economy" and is undoubtedly influenced by his selection of Verhoeff's system of classification. The dismissal of difficulties of variation by attributing them to "adaptations to a modus vivendi" seems to be evading the issue. Evolutionary mechanisms are being better understood today to make that line of argument more and more tenuous. It is the author's hope that the neglected chilopods will receive more attention in the future. Only then will the existing arguments about their phylogeny be tested.

VI. SUMMARY

1. The anatomy of the cephalic nervous system of *Arenophilus bipuncticeps* (Wood) was studied. Serial sections were prepared and studied with trichrome and silver impregnation techniques. Graphical reconstructions were made to demonstrate the more gross relationships. Photographic methods aided in the interpretation of microscopic relationships.

2. The brain, or supraesophageal ganglion, is composed of a protocerebrum, a deutocerebrum, and a tritocerebrum, which may be distinguished histologically. Grossly, however, they are fused into a single mass. The brain is connected to a subesophageal ganglion by long, cordlike circumesophageal connectives. Both ganglia are composed of a cellular cortex and a fibrous core. The constituents are bilaterally symmetrical in number and position.

3. The cephalic nerves emerge from the three neuromeres of the brain and subesophageal ganglion and are homologized with those of other chilopods. A cerebral gland is associated with the frontal lobes of the protocerebrum. The nerve to the gland exhibits possible neurosecretory significance. Nerves supplying the intrinsic and extrinsic musculature of the antennae were traced to their nuclei of origin located ventrally in the deutocerebrum. The recurrent nerve

emerges from a stomatogastric bridge which is poorly developed and incorporated in the ventral portion of the brain. Other nerves emerging from the supraesophageal and subesophageal ganglia are described.

4. The neurohistology of *bipuncticeps* was studied. The cellular cortex of the ganglia contains cells whose processes turn inward to form part of the fibrous medullary neuropile. The neurilemmal elements consist of an outer homogeneous "neural lamella" and a cellular "perilemma" containing at least three types of cells. Motor neurons, associational neurons, and neuroglial cells may be differentiated on the basis of staining qualities. Four "giant" cells, possibly of a neuroglandular nature, are present in the anteroventral portion of the subesophageal ganglion.

5. Fibrous entities in the neuropile were examined and homologized. "Antennal glomeruli," the "corpus lamellosum," and "olfactorio-globularis tract" are identified. Connections between the antennal lobes and subesophageal ganglion are observed. The "corpora pedunculata" and "central complex" do not appear in *bipuncticeps*, and it is highly improbable that there exist vestiges or Anlagen of these complex elements in the geophilomorph brain. The commissures located in the median plane are homologized with the named commissures of higher chilopods.

6. The cephalic nervous system of *bipuncticeps* is simply organized and less complex than those in the other orders of the Chilopoda.

ABBREVIATIONS USED ON THE FIGURES

a,b,c, three types of perilemmal nuclei.	D, deutocerebrum.
ADC, anterior commissure of D.	DC, deutocerebral commissure.
AL, antennal lobe.	DI, Dm, lateral, medial lobe of deutocerebrum.
ANT, antenna.	exo, exoskeleton.
ax, axon of giant cell in SBG.	ff ₁ , fibers of nerve to intrinsic antennary musculature emerging from the neuropile.
bv, haemolymph vessel associated with the cerebral gland.	ff ₂ , fibers from nucleus of origin of N ₆ .
bn, black-staining neuroglial nucleus.	ff ₃ , fibers from the pars intercerebralis.
CBV, cerebral haemolymph vessel.	ff ₄ , fibers from frontal lobe in the large protocerebral commissure.
CC, central complex.	FG, frontal ganglion.
CGL, cerebral gland.	FL, frontal lobe.
clm, corpus lamellosum.	gcn, giant cell nucleus.
CLYP, clypeus.	
COES, commissure of circumesophageal connectives.	
CPL, cephalic plate.	

- gl, portion of medial buccal gland.
glom, large antennal glomerulus.
HYP, hypopharynx.
LBR, labrum.
LPC, large protocerebral commissure.
mm, muscle fibers.
MND, mandible.
MX₁, first maxilla.
MX₂, second maxilla.
MXP, prehensor.
N₄, nerve to cerebral gland.
N₅, nerve from brain to frontal ganglion.
N₆, sensory nerve to clypeus.
N₇, antennal nerve.
N₈, nerve to ventral extrinsic antennary musculature.
N₁₁, nerve to dorsal extrinsic antennary musculature.
N₁₃, stomatogastric bridge.
N₁₄, recurrent nerve.
N₁₆, nerve to longitudinal clypeal musculature.
N₁₇, labral nerve.
N₁₈, nerve to lateral portion of oral opening.
N₂₀, nerve from which N₁₈ and N₁₉ originate.
NMD, nerve to mandible.
NMX₁, nerve to first maxilla.
NMX₂, nerve to second maxilla.
NNIM, nerve bundles to intrinsic antennary musculature.
np, neuropile.
OEC, circumesophageal connective.
OES, esophagus.
OP, optic lobe.
P, protocerebrum.
PB, protocerebral bridge.
PDC, posterior commissure of D.
PI, pars intercerebralis.
PI[AL], PI of antennal lobe.
pn, pink-staining neuroglial nucleus.
SBG, subesophageal ganglion.
sp, neurosecretory product (?) in giant cell.
STG, stomatogastric ganglion.
T, tritocerebrum.
TR, trachea.
tr, tracheole.

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EXPLANATION OF PLATES

PLATE 1

The cephalic nervous system of *Arenophilus bipuncticeps* (Wood) showing the levels at which the sections seen in the following photomicrographs were taken. *Inset*, transverse section of the right antennal nerve showing the three nerve bundles which innervate the intrinsic antennary musculature. The two ventral bundles and one dorsolateral bundle are more heavily stained and enclosed in their own neurilemma (not seen in silver preparations but verified in general trichrome stains).

PLATE 2

FIG. 1. Transverse section through the antennal lobes, showing the fibers (ff_1) of the ventral bundle of nerves which innervate the intrinsic antennary musculature. The large antennal glomerulus (glom) is ventrally situated.

FIG. 2. Transverse section through the antennal lobes showing the fibers (ff_2) from the nucleus of origin of N_3 (located immediately to the left of ff_2). PI[AL] is the pars intercerebralis of the fused antennal lobes.

FIG. 3. Transverse section showing the lateral and medial lobes of the deutocerebrum (DL, Dm). The interior of the corpus lamellosum (clm) is weakly stained but can be identified by its arrangement of parallel fibers.

PLATE 3

FIG. 1. Transverse section through the deutocerebral lobes showing the fibers (ff_3) from the cells in the pars intercerebralis (PI) entering the corpus lamellosum (clm).

FIG. 2. Transverse section showing the narrow band of fibers of the protocerebral bridge (PB) forming a commissure dorsal to the cerebral blood vessel (CBV). The frontal lobe is dorsal and lateral to the deutocerebrum (D). The stomatogastric ganglion, ventral to the cerebral blood vessel is damaged and out of focus.

FIG. 3. Section immediately following that illustrated in figure 2. The stomatogastric ganglion (STG) sends fibers into each of the cerebral hemispheres, intercommunicating the two halves of the deutocerebrum.

PLATE 4

FIG. 1. Section through the large protocerebral commissure (LPC) showing fibers (ff_4) intercommunicating the frontal lobes. Seen in cross section are muscle fibers (mm) of the *levator pharyngis* immediately ventral to the median recurrent nerve (N_{14}).

FIG. 2. Section showing the recurrent nerve (N_{14}) flanked by the paired labral nerves (N_{17}). The arcuate fibers dorsal to the cerebral blood vessel are those of the commissure of the circumesophageal connectives (COES).

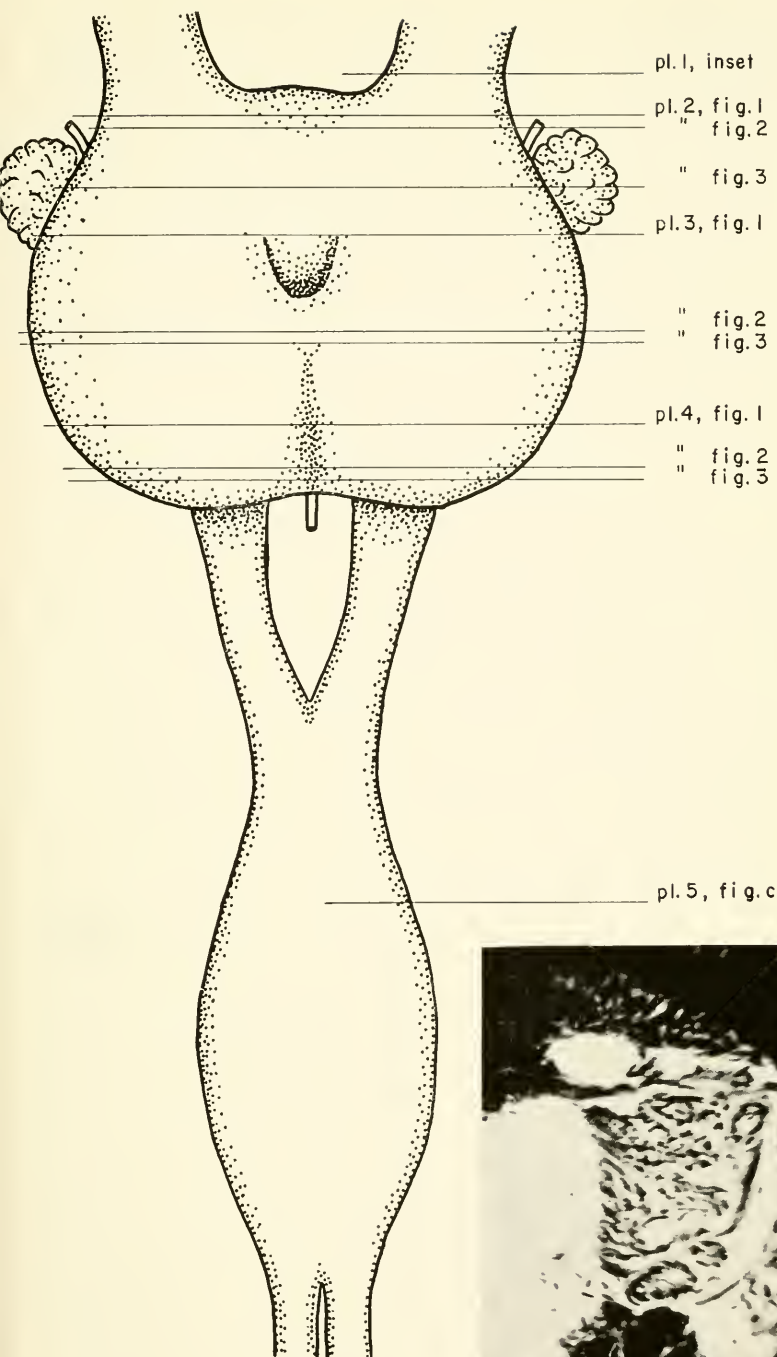
FIG. 3. Section showing the base of the brain and the circumesophageal connectives (OEC). Note that the cellular cortex is beginning to envelop the neuropile of the connectives dorsally, thus delimiting them from the caudal portion of the supraesophageal ganglion.

PLATE 5

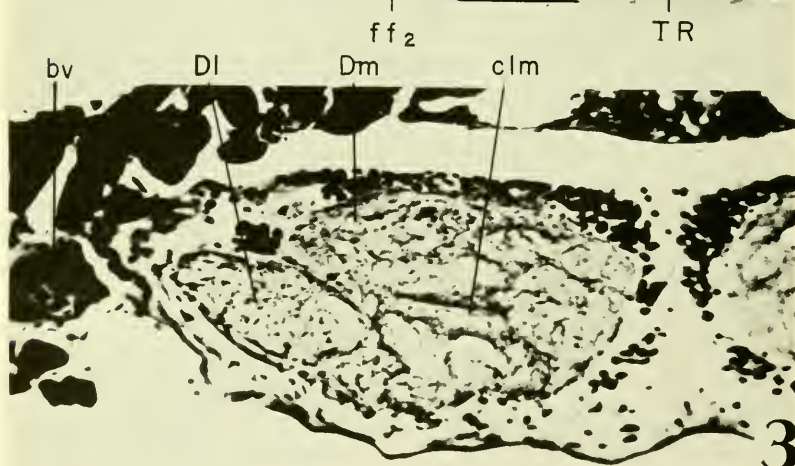
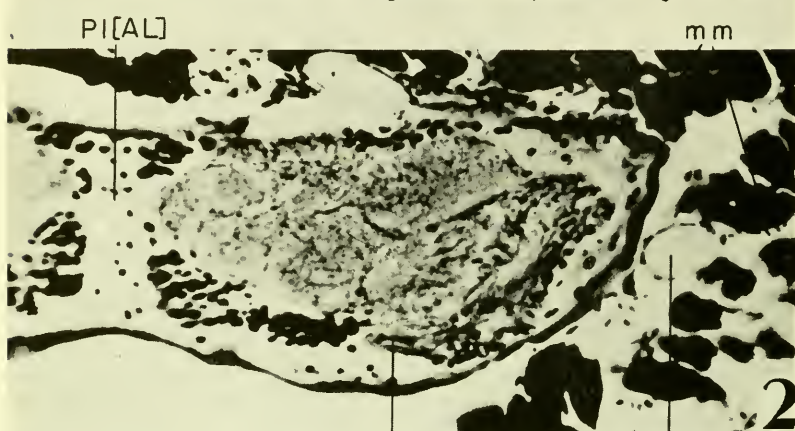
FIG. A. Showing the three types of nuclei (*a, b, c,*) found in the inner cellular perilemmal portion of the neurilemma. A portion of a tracheole (*tr*) is seen to the left with its small nucleus (out of focus) adhering to the periphery.

FIG. B. The two types of neuroglial nuclei in the neuropile. One type (*pn*) has pink staining chromatin with an exocentric nucleolus; the other (*bn*) has densely aggregated black staining chromatin. The dimensions of the first type may serve as a scale for this and the preceding figure (3×5 microns).

FIG. C. A transverse section through a giant cell located in the subesophageal ganglion. The large nucleus possesses a centrally situated clump of chromatin (*gcn*). A tracheole (*tr*) which may be mistaken for a second giant cell process is seen to the left of the axon (*ax*). The mass of material ventral to the nucleus (*sp*) may be a secretory product of the giant cell. The dimensions of the nucleus are approximately 12×20 microns.

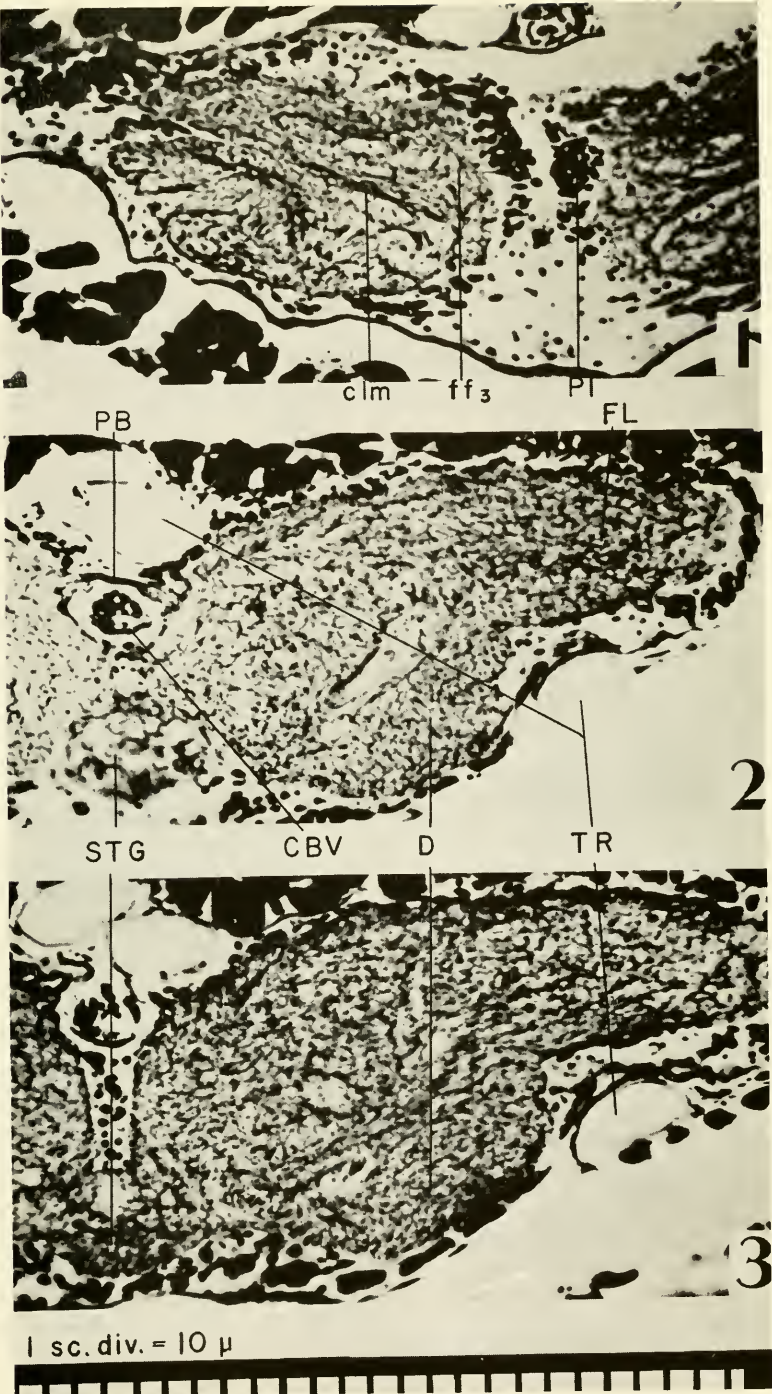


(See explanation of plates at end of text.)

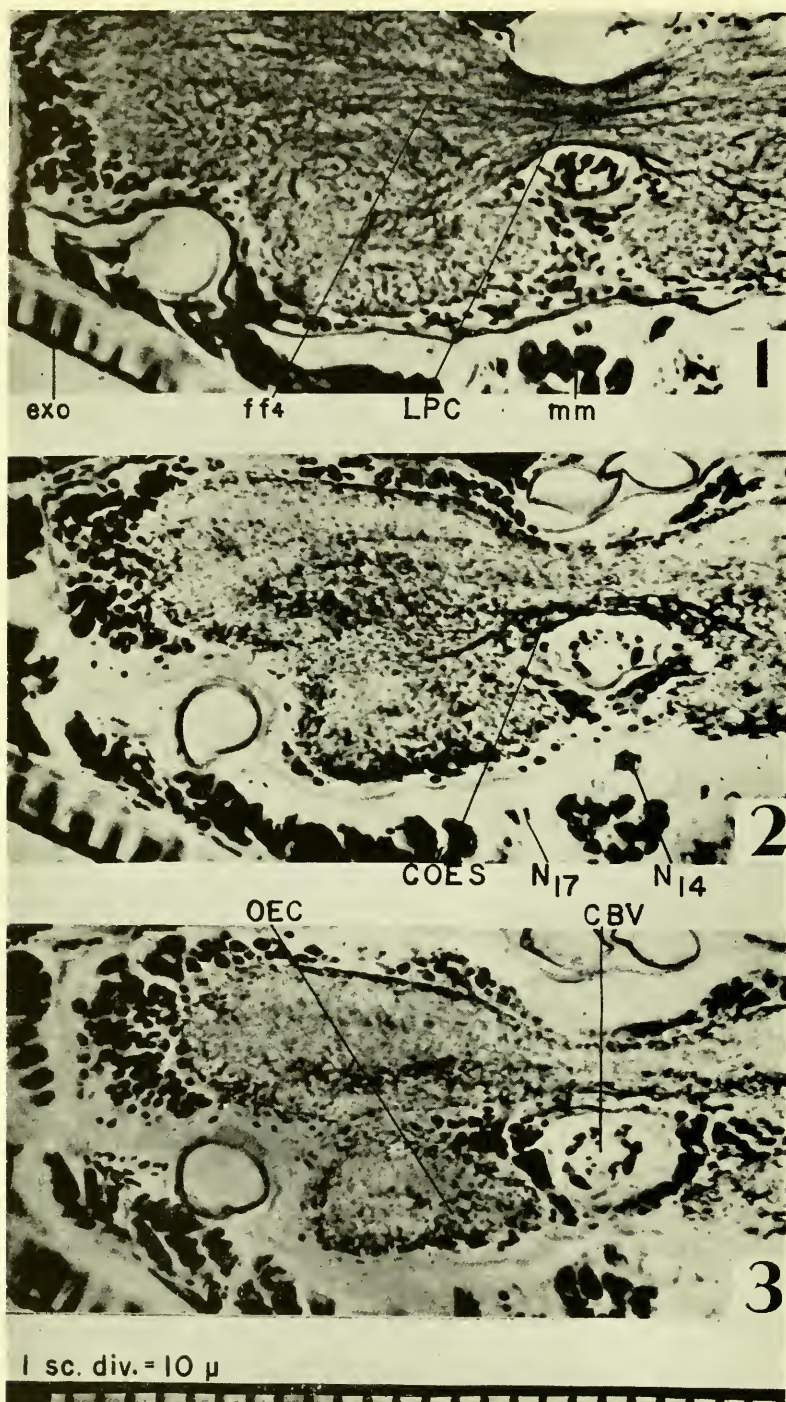


1 sc. div. = 10 μ

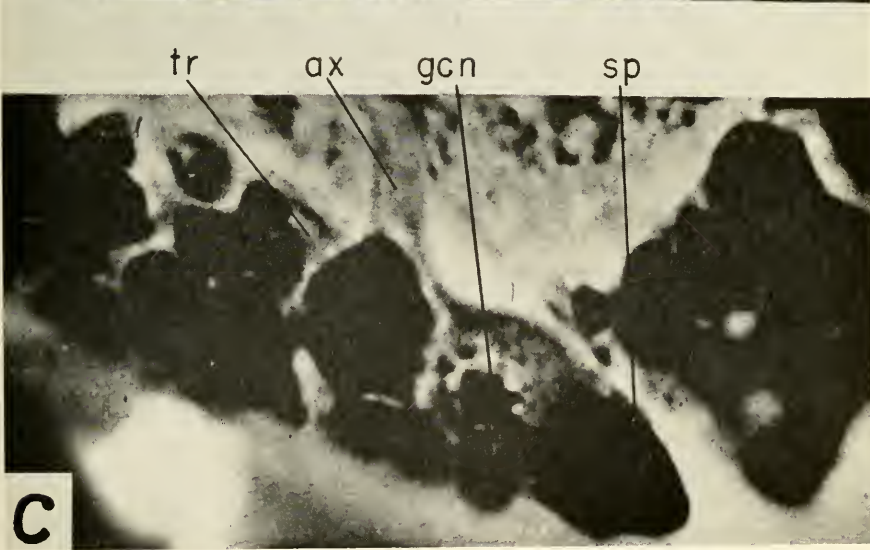
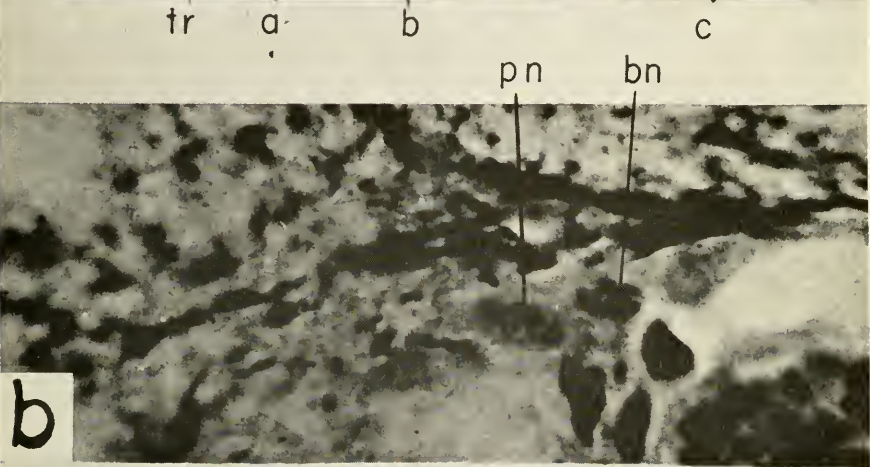
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SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 140, NUMBER 5
(END OF VOLUME)

Charles D. and Mary Vaux Walcott
Research Fund

A REVISION OF THE ORDOVICIAN
BRYOZOAN GENERA BATOSTOMA,
ANAPHRAGMA, AND AMPLEXOPORA

(WITH SEVEN PLATES)

By
RICHARD S. BOARDMAN
Associate Curator of Geology
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(WITH SEVEN PLATES)

INTRODUCTION

The genera *Batostoma* Ulrich, 1882, *Anaphragma* Ulrich and Bassler, 1904, and *Amplexopora* Ulrich, 1882, all belong to the order Trepostomata of the Bryozoa. The three genera are here grouped together merely as a convenience in discussing their mutual problems. The grouping does not necessarily imply close taxonomic relationships among the genera.

The genera *Batostoma* and *Anaphragma* are placed in the family Trematoporidae Ulrich in Miller, 1889 (Bassler, 1953, p. 6113). *Batostoma* is a fairly common genus in Middle and Upper Ordovician rocks of North America. *Anaphragma* is known only from rocks of Richmond age in North America and highest Middle and Upper Ordovician rocks in Estonia. *Anaphragma* was described originally as, "agreeing in all essential respects with *Batostoma* Ulrich, except that both the zooecial tubes and mesopores are entirely devoid of diaphragms" (Ulrich and Bassler, 1904, p. 49). Based on the study of newly made thin sections of types, all internal characters of generic value are interpreted here to be dissimilar in the two genera (see p. 12).

The genus *Amplexopora* is the type genus of family Amplexoporidae Ulrich in Miller, 1889. Restudy of the primary types in the U. S. National Museum collection resulted in approximately half of the species previously placed in *Batostoma* being reassigned to *Amplexopora*, and this in turn doubled the number of species of *Amplexopora* in the collection. If these reassignments prove to be valid,

the resulting picture of morphologic trends and hypothesized lineages discussed below suggest that species of *Amplexopora* will prove extremely useful in stratigraphic paleontology.

The genus *Stromatotrypa* Ulrich, 1893, was investigated in connection with *Batostoma*, and study of new sections of the type species, *S. ovata* Ulrich, 1893, resulted in *Stromatotrypa* being considered a junior subjective synonym of *Batostoma*. (See p. 6 and pl. 7, figs. 2-4.)

The genus *Acanthotrypella* Vinassa de Regny, 1920, was considered to be a junior subjective synonym of *Batostoma* by Bassler (1935a, p. 54). Study of new sections of the type species, *B. variable* Ulrich, 1890, resulted in *Acanthotrypella* being considered a junior subjective synonym of *Amplexopora*. (See p. 19 and pl. 7, fig. 1.)

The manuscript was critically read by June Phillips, Yale University, N. Spjeldnaes, University of Oslo, and R. Cifelli and P. M. Kier, U. S. National Museum, and many of their suggestions have been incorporated in the final draft. Thin sections were prepared by T. M. Robison of the U. S. Geological Survey. Photography was done by J. Scott of the U. S. National Museum.

Wall structure and ontogeny of Anaphragma.—The thin zooecial walls in the endozones (immature or axial region of authors) of most trepostomes are either granular or longitudinally laminated and give no indication of whether their deposition took place from one or both sides of the walls. The zooecial walls in the endozones of the type species of *Anaphragma*, *A. mirabile* Ulrich and Bassler, 1904, are laminated and contain a dark median line that is connected distally to zooecial boundaries in the exozones (mature or cortical region of authors). These median lines are interpreted as zooecial boundaries in the endozones and are considered to indicate that the walls are transversely laminated and that deposition of the walls took place from both sides (Boardman, 1959, p. 2). Thus, the structure of the walls in the endozones of *A. mirabile* is thought to support the logical assumption that the walls result from deposition by tissue of immediately adjacent zooecia.

The microstructure and resulting appearance of zooecia, mesopores, and acanthopores of *A. mirabile* show progressive changes of remarkable magnitude through a thick-walled exozone. The zooecia are assumed to have grown by the addition of skeletal laminae on the surfaces at their distalmost ends, thus adding to the width of the exozone. The width of the exozone in a segment of a fossil zoarium

then is assumed to be approximately proportional to the ontogenetic growth stage or stages attained by the individual asexual zooids at their death. In the Trepostomata, a progressive decrease in the width of the exozone and number of zooecial diaphragms is generally observable from bottom to top of essentially complete zoaria of appreciable vertical extent such as ramose, frondescent, or bifoliate growth habits. The ontogenetic stage attained by the oldest zooids at the base of a colony then provides a measure of the astogenetic stage of the colony as a whole, and the progressive decrease in exozone width and number of diaphragms up through the colony to the growing tips indicate subsequent addition of progressively younger zooids.

A significant change in microstructure of zooecia as individuals within a colony grew distally is not common in exozones of the Trepostomata, so an estimate of ontogenetic stage is not generally possible in tangential sections that cut zooecia and acanthopores transversely. In *A. mirabile*, however, zooecial walls change from an integrate appearance with sharply defined zooecial boundaries to broadly amalgamate with obscure boundaries. Also, wall laminae change from a V-shaped to broadly U-shaped configuration in most zooecia, and acanthopores start with very small diameters and become progressively larger until they dominate cross-sectional shapes of mesopores and some zooecia (pl. 4). The variation is unusually large and a reasonably large number of specimens is necessary to demonstrate intermediate forms and to correlate variation with stage of development of individual zooecia.

Stratigraphic occurrence of offset acanthopores in Amplexopora.—The species restudied and included in *Amplexopora* in this paper occur in the Middle and Upper Ordovician series. All these species have acanthopores that extend through the exozones and are concentrated in zooecial corners, very similar to conservative acanthopores occurring throughout the order Trepostomata. In addition, the type species and most of the other Upper Ordovician species contain a second, more distinctive type of acanthopore that extends through only a part of the exozone width, is concentrated between zooecial corners, and is offset from the zooecial boundaries toward the voids of the zooecia resulting in inflection of the zooecial walls (see pl. 5, fig. 2). In extreme development, such inflection gives a petaloid or septate appearance to zooecia as seen in cross section in tangential thin sections. The superficial likeness of the offset acanthopores to radially arranged septa led Ulrich to term these acanthopores "pseudo-

septa" in the original description of the type species, *A. septosa* (Ulrich, 1879, p. 125). (For further description of offset acanthopores see pp. 19, 21.)

Of the approximately 18 Middle Ordovician species of *Amplexopora*, described and undescribed, in the U. S. National Museum collections, offset acanthopores causing inflection of zooecial walls are limited to a single undescribed species from the Cannon limestone near the top of the Trenton, Pulaski, Giles County, Tenn.

Of the approximately 14 Upper Ordovician species of *Amplexopora*, described and undescribed, in the U. S. National Museum collections, offset acanthopores causing inflection of zooecial walls were found in all but one species, *A. variable* (Ulrich), 1890, from the top of the Richmond group, Osgood, Ind.

Most of the Middle and Upper Ordovician species of *Amplexopora* referred to above have been described or differentiated on one to several sectioned specimens and are therefore necessarily typological in taxonomic approach. Despite the theoretical limitations of typologically defined species, enough specimens are available to indicate that offset acanthopores are characteristic of *Amplexopora* in the Upper Ordovician rocks of the Ohio and Mississippi River valleys.

Within the present concept of *Amplexopora* at least three inferred lineages appear concurrently in rocks of Middle and Upper Ordovician age in North America. One lineage is characterized morphologically by *A. conferta* (Coryell) of Black River age, *A. cylindracea* Ulrich and Bassler of Trenton age, and *A. columbiana* Ulrich and Bassler, of Maysville age, and seems to be geographically centered in the Central Basin region of Tennessee. The Upper Ordovician species in this first lineage develop offset acanthopores but not as strongly as those occurring in a second lineage characterized by the type species, *A. septosa* (Ulrich). This second lineage seems to be centered in the Ohio, Indiana, and northern Kentucky region, but this impression is no doubt partly due to the predominance of collections from that area in the Museum's Upper Ordovician material.

A third lineage is suggested by species such as *A. winchelli* Ulrich from the Decorah shale in the Upper Mississippi Valley and *A. cingulata* Ulrich and *A. robusta* Ulrich in formations of the Maysville group in the Ohio, Indiana, and northern Kentucky region. In this third lineage, the Upper Ordovician species develop offset acanthopores, which are so small in diameter that they rarely produce an extreme petaloid or "pseudo-septal" appearance in tangential sections.

SYSTEMATIC DESCRIPTIONS

Genus **BATOSTOMA** Ulrich

1882. *Batostoma* Ulrich, Journ. Cincinnati Soc. Nat. Hist., vol. 5, pt. 1, p. 154; pt. 2, p. 256.
1890. *Batostoma* Ulrich, Illinois Geol. Survey, vol. 8, pp. 379, 459.
1893. *Batostoma* Ulrich, Geology of Minnesota, vol. 3, pt. 1, pp. 288-290.
1893. *Stromatotrypa* Ulrich, Geology of Minnesota, vol. 3, pt. 1, pp. 301, 302.

Type species.—*Monticulipora (Heterotrypa) implicatum* Nicholson, 1881, by monotypy.

Emended definition.—Zoaria are ramose or incrusting and moniticules are generally low. Zooecial walls in the endozones are thin, dark, and granular and are connected directly with the well-defined, dark, granular, slightly serrated zooecial-mesopore boundaries of the exozones. In the exozones, zooecia are generally oval in cross section and contain thin, laminated, irregularly spaced diaphragms. As seen in longitudinal sections, the laminae of adjacent zooecial walls lie nearly parallel to the zooecial boundaries, then curve distally just before intersecting the boundaries to form a V-shaped pattern that has extremely long, convexly curved limbs. In tangential sections, walls of adjacent zooecia are generally integrate in appearance.

Mesopores are polygonal in cross section, filling the spaces between zooecia. Laminated wall material on the mesopore sides of boundaries is generally thinner than on zooecial sides, and is lacking entirely in earlier growth stages of several species. Mesopores contain closely spaced diaphragms that generally are curved convexly outward. Larger mesopores have more than one longitudinal row of curved diaphragms that together form a flattened cystose pattern. Mesopore diaphragms are generally thicker than those in zooecia and consist of a thin, dark, granular layer on proximal sides and a thicker laminated layer on distal sides. Acanthopores are variable in size and abundance, and in a few species are very rare.

Discussion.—Based on an examination of thin sections of primary types of species now assigned to *Batostoma* in the U. S. National Museum collections, the following species are considered to belong to that genus:

- B. cumingsi* Loeblich, 1942, Bromide formation, Middle Ordovician, Oklahoma.
B. fertilis Ulrich, 1886, lower half of the Trenton shales, Middle Ordovician, Minnesota.
B. fertile var. *circulare* Ulrich, 1893, lower third of the Trenton shales, Middle Ordovician, Minnesota.
B. manitobense Ulrich, 1889, Stony Mountain formation, Upper Ordovician, Manitoba.

- B. maysvillense* Nickles, 1905, Mount Hope shale member of the Fairview formation, Upper Ordovician, Maysville, Ky.
B. prosseri Cumings and Galloway, 1912, Waynesville and Liberty formations, Upper Ordovician, Ind.
B. varium Ulrich, 1893, middle third of Trenton shales, Middle Ordovician, Minneapolis, Minn.

The holotype sections of *B. inutilis* Coryell, 1921, and *B. ramosa* Coryell, 1921, both from the Pierce limestone of Tennessee, and *B. humile* Ulrich, 1893, from the Galena shales, Minnesota, were made from fragments of zoaria that contained early stages of development, and generic affinities are not clearly demonstrated. These species are retained in the genus until additional material can be studied.

The primary types of *Batostoma magnopora* Ulrich, 1893, are silicified and structures are insufficiently preserved to identify the specimens generically.

For a list of species originally placed in *Batostoma* that compare closely with the genus *Amplexopora* and are here reassigned to that genus, see page 18.

The type species of *Stromatotrypa* is *S. ovata* Ulrich, 1893, by original designation. The primary types of *S. ovata* (U.S.N.M. 43614) are from the *Rhinidictya* beds (approximately the middle third) of the Decorah shale, Minneapolis, Minn. Sections of previously unsectioned cotypes agree with the two cotypes that had been sectioned, and all are considered to be thin-walled incrusting forms of the genus *Batostoma* (pl. 7, figs. 3, 4). Reexamination of sections of the type species of *Batostoma*, *B. implicatum* revealed a short section of conspecific overgrowth having walls comparable in thickness (pl. 7, fig. 2) with those of *S. ovata*. All qualitative generic characters of *Batostoma* are present in *S. ovata*, including comparable wall structure, arrangement and shape of zooecia and mesopores, and the convexly curved diaphragms in mesopores. Perhaps most significant are the notched acanthopores with structureless cores that are found in *S. ovata* (pl. 7, fig. 3b), the type species of *Batostoma*, and most, but not all, of the other species of *Batostoma*. This type of acanthopore is very rare in the Trepostomata, occurring in one other genus of the order as now understood.

Also of importance, but only suggestive of the real nature of *S. ovata*, is one of the newly sectioned cotypes consisting of a complicated incrusting growth on the branch of a specimen of *B. varium* Ulrich, the primary types of which are also from the Middle Decorah shales

of Minneapolis. All the incrusting growth included in the thin section appears to be overgrowth conspecific with the supporting branch of *B. varium*. Species characters of incrusting forms and overgrowths are generally extremely variable, owing at least in part to compensations made necessary in covering rough, irregular surfaces. It is possible to say only that the overgrowth on the specimen of *B. varium* could be within the morphologic range of the other primary types of *S. ovata*. The other primary types of *S. ovata* incrust other genera of Bryozoa and so are true incrusting growths. A detailed study of many topotypes is necessary to clarify the relationships between the two species. On the basis of comparison of presumed generic characters, however, *Stromatotrypa* is here considered to be a junior subjective synonym of *Batostoma*, and *S. ovata* is reassigned to *Batostoma*.

Two other species in the National Museum collections have been assigned to *Stromatotrypa*. The primary types of *S. globularis* Ulrich and Bassler, 1913, Keyser limestone member of the Helderberg limestone, West Virginia and Maryland, are badly silicified and resectioning of the types has not revealed sufficient characters to reassign the species. *S. frondosa* Loeblich, 1942, from the Bromide formation, Oklahoma, is closely comparable with *B. prosseri* Cumings and Galloway, 1912, and both species are placed in *Batostoma* with some uncertainty.

BATOSTOMA IMPLICATUM (Nicholson)

Pl. 1, figs. 1-5; pl. 2, figs. 1-4; pl. 7, fig. 2

1881. *Monticulipora (Heterotrypa) implicatum* Nicholson, The genus *Monticulipora*, p. 147, pl. 2, figs. 7-7e, text fig. 27.
1882. *Batostoma implicatum* (Nicholson), Ulrich, Journ. Cincinnati Soc. Nat. Hist., vol. 5, pt. 2, p. 256.
1908. *Batostoma implicatum* (Nicholson), Cumings, Indiana Dept. Geol. and Nat. Res. 32d Ann. Rep., p. 774, pl. 7, fig. 7; pl. 8, fig. 2.

Type data.—The species was first named in a faunal list by Ulrich (1880, p. 12) but no indication, definition, or description was included. The list dealt with the fauna about Cincinnati, and Ulrich reported the species from the 100- to 200-foot interval above the low-water mark of the Ohio River. This interval now forms the greater part of the Southgate member of the Latonia shale of the Eden group (Bassler, 1906, p. 8; 100 to 220 feet above the low-water mark). In 1881, Nicholson published a description of the species based on specimens received from J. M. Nickles of Cincinnati, a close associate of Ul-

rich. The locality was given by Nicholson as "Cincinnati Group, Ohio," and the depository of the primary types is unknown.

Material studied.—The assumption is made here that the primary types came from the Southgate member in the Cincinnati region. The description below is based on specimens from that member identified as *B. implicatum* in the U. S. National Museum collections, plus specimens collected by the author, as follows:

U.S.N.M. 2994: Southgate member, Chesapeake and Ohio Railroad cut on northeast slope of Bald Knob on west side of Mill Creek, Cincinnati, Ohio, collected by R. Boardman. Sections from 9 fragmentary zoaria studied.

U.S.N.M. 2995: Southgate member, 150 feet above river, head of Monmouth Street, Newport, Ky. Collector unknown. Sections from 9 fragmentary zoaria were studied.

U.S.N.M. 2999: Southgate member, Shadwell Street, Cincinnati, Ohio. Collector unknown. Sections from 10 fragmentary zoaria were studied.

U.S.N.M. catalog numbers of illustrated specimens are 138266-138272.

Description.—Zoaria are ramose, incrusting, or a combination of these two growth habits. Branches are circular to elliptical in cross section. Secondary overgrowth is characteristically well developed on ramose zoaria, as many as four layers occurring on older branches. Irregular development of overgrowths, especially their ramose extensions beyond primary branches, produces anastomosing branches that display erratic and confused zooecial growth at surfaces where branches are joined. Lateral branches arising from overgrowths are commonly discordantly small in diameter and random in arrangement. Local patches of more extended zooecial growth or abrupt changes in direction and diameter of secondary branches beyond the ends of primary branches produce localized swellings on the branches that are characteristic of the species.

Monticules are generally flush with the surface of the zoarium and the monticular zooecia are little different from intermonticular zooecia.

In the endozone, zooecial walls are thin, dark, and somewhat granular in appearance. The zooecia are extremely variable in width and irregular in direction, bending in and out of the planes of longitudinal thin sections. Partitions transverse to the zooecia are common but irregularly distributed and are planar or curved. Many zooecia seem

to originate at transverse partitions, either one large zooecium becoming two at the partition, or two zooecia becoming one.

In the exozone, the species is characterized by an irregularity of gross structures and poorly defined microstructure that is uncommon in trepostomes. Walls between adjacent zooecia or adjacent zooecia and mesopores are delimited by boundaries that in longitudinal sections are well defined, dark, granular, slightly serrated lines or zones. The boundaries are located at the points at which laminae from adjacent walls abut. Laminae of zooecia and mesopores are generally difficult to distinguish and intersect the boundaries at angles of less than 90 degrees to form the V-shaped pattern characteristic of the genus. Diaphragms in the zooecia are generally thin, laminated, slightly curved to planar, and widely and irregularly spaced. Cystoidal diaphragms are few.

Mesopores are common between zooecia although they rarely surround the zooecia completely. The mesopores contain thick, closely spaced diaphragms that are generally curved convexly outward. Larger mesopores have more than one longitudinal row of diaphragms; the rows are separated by the diaphragms themselves curving back proximally through 90 degrees to form an irregular, flattened, cystose pattern. The proximal sides of mesopore diaphragms display a dark granular layer of material similar in appearance to the material of the zooecial walls in the endozones and the zooecial boundaries in the exozones. This dark layer is connected directly to the boundaries between the mesopores and adjacent zooecia in many mesopores. The distal sides of the mesopore diaphragms are thicker than the proximal dark layer and are composed of laminated material similar in appearance to that of the zooecial walls. The laminated material thins rapidly as it bends either proximally with the diaphragms in the center of a mesopore, or distally along the wall of a mesopore. Thus, the laminated material on the mesopore side of the wall is either lacking or much thinner than the laminated deposit of relatively constant thickness on the zooecial side of the boundary.

Acanthopores are conspicuous in longitudinal sections and characteristically display a large core of structureless, transparent calcite. The cores have sharply notched sides caused by the unequal extensions of laminae into them from the surrounding laminated material of the zooecial walls. A few acanthopores appear to have very short lateral branches.

In tangential sections, younger ontogenetic stages of development,

as seen in young branches or in deep tangential sections of older branches, have a different appearance than older stages of development, as seen in shallow sections of older branches. In younger stages, the dark, granular, zooecial-mesopore boundaries are easily visible and in tangential sections appear as straight lines between zooecia and straight or curved lines between zooecia and adjacent mesopores. The curved boundaries are convex toward the mesopores, producing irregular, compressed, subpolygonal cross sections in the mesopores and subpolygonal to subcircular boundaries in the zooecia. In these younger stages the mesopores are open, having little or no laminated tissue on the mesopore walls inside the boundaries. The mesopores appear to be merely open spaces between the zooecia. The zooecia contain a thick laminated deposit inside the boundaries that smooth out the polygonal configurations of the boundaries and produce generally oval zooecial voids.

In tangential sections older growth stages are characterized by a general thickening of skeletal material in zooecia and mesopores. The dark zooecial-mesopore boundaries are largely obscured, zooecial walls are thickened, reducing the diameters of zooecial voids, and mesopores are generally filled with skeletal material originating either from the mesopore walls or a combination of walls and diaphragms. The filling of mesopores makes their numbers obscure in tangential sections in older growth stages.

Acanthopores in tangential sections are randomly arranged on the zooecial boundaries. Many appear transparent and structureless, a few show the concentric laminae more typical of the Trepostomata. Acanthopores are extremely variable in number and diameter from zoarium to zoarium, and within a few zoaria are extremely variable in diameter. Many acanthopores, regardless of diameter, cause inflection of zooecial walls. There seems to be little correlation between zooecial wall thickness and acanthopore diameter, the tangential sections through older growth stages with thick walls can have either large, small, or variable acanthopores. This variability in diameter of acanthopores is at least partly controlled by the notched character seen in longitudinal sections.

Monticules in tangential sections are either concentrations of several filled mesopores or zooecia that are slightly larger in diameter than intermonticular zooecia.

Quantitative data.—The following tables are based on sections from 25 fragmentary zoaria that are thought to be topotypes of Nicholson's original specimens. All measurements are in millimeters.

The axial ratio is the ratio of the diameter of the endozone to the corresponding branch diameter.

TABLE 1.—*General measurements*

	Maximum	Minimum
Diameter of zoarium.....	9.1	4.4
Diameter of endozone.....	5.1	2.5
No. zooecia in 2 mm. (longitudinal direction).....	6½	5
Average major axis of zooecial void per fragment... 0.30		0.23
Acanthopores per zooecium.....	3.5	0.6

TABLE 2.—*Ontogeny*

Average No. diaphragms in zooecium	Width of exozone	Axial ratio
1-2	1.2-1.6	0.64-0.74
3	2.3	0.60
5	2.2-2.5	0.56-0.67
6	2.6-2.8	0.49-0.56
8	3.3	0.57
9	4.4	0.52
12	4.8	0.44

Genus ANAPHRAGMA Ulrich and Bassler

1904. *Anaphragma* Ulrich and Bassler, Smithsonian Misc. Coll., vol. 47, No. 1470, p. 49.
 1911. *Anaphragma* Ulrich and Bassler, Bassler, U. S. Nat. Mus. Bull. 77, p. 297.
 1920. *Batostoma* (*Anaphragma*) Ulrich and Bassler, Vinassa de Regny, Atti Soc. Ital. Sci. Nat., vol. 59, p. 226.
 1935a. *Anaphragma* Ulrich and Bassler, Bassler, Fossilium Catalogus, I: Animalia, pars 67, p. 46.

Type species.—*Anaphragma mirabile* Ulrich and Bassler, 1904, by original designation.

Emended definition.—Zoaria are ramose. Zooecial walls in endozones range from straight to crenulated, are laminated, and generally display dark zooecial boundaries. In the exozone, laminae of zooecial walls generally form a U-shaped pattern in longitudinal sections, but a V-shaped pattern is common in walls of early exozones and occurs throughout the length of zooecia in some zoaria. Thin, complete diaphragms are sparsely distributed, one to several in a very few zooecia; most zooecia completely lack diaphragms.

In tangential sections, zooecial walls are generally amalgamate, but can be integrate in appearance. Laminated acanthopores are common; their size can be extremely variable within a species.

Mesopores are common, have walls comparable in thickness with zooecia, and are generally without diaphragms.

Discussion.—*Anaphragma* is described in the literature as agreeing in all essential respects with *Batostoma*, except for very few diaphragms in zooecia and mesopores and crenulated zooecial walls in the endozone. The phyletic histories of *Anaphragma* and *Batostoma* are not known at present, so the relationships between the two genera

TABLE 3.—*Summary of generic characters distinguishing Anaphragma and Batostoma*

<i>Structures in common</i>	<i>Batostoma</i>	<i>Anaphragma</i>
Endozone	Uniformly thin and granular	Variable in thickness, laminated with visible zooecial boundaries
Exozone wall laminae ..	V-shaped pattern	U-shaped, rarely V-shaped pattern in older growth stages
Zooecial boundaries	Well defined throughout	Obscured in older growth stages
Zooecial walls in tangential view	Integrate	Amalgamate, except in a few zooecia in youngest growth stages
Mesopore walls	Laminated material lacking in earlier growth stages, generally thinner than that of adjacent zooecia in later stages	Laminated material comparable in thickness with zooecia throughout
Acanthopores	Generally filled with transparent calcite and in many species sides are notched. Diameter not greatly controlled by growth stage	Laminated and obscure in longitudinal sections. Diameter largely controlled by growth stage in type species

must be evaluated on morphologic comparisons alone. Further sectioning of the cotype suite and topotypes of *A. mirabile* indicate that the only comparable character the two genera share, as the genera are presently understood, is a distressing external homeomorphy, as witnessed by five previously unsectioned specimens of *Batostoma* sp. in the cotype suite of *A. mirabile*. Table 3 summarizes the generic descriptions of structures that the two genera have in common. It is not impossible, of course, for one of the generic stocks to have developed from the other, but on the basis of our limited data the external homeomorphy seems fortuitous and there is no evi-

dence for a phyletic or descriptive relationship between the genera.

The collection of the U. S. National Museum also includes a species of *Anaphragma* identified as *A. mirabile* from the Fernvale formation near Pulaski, Tenn., and two other forms of *Anaphragma* identified as *A. mirabile* Bassler, 1911 (p. 298) and *A. mirabile cognata* Bassler, 1911 (p. 299), from the highest Middle and Upper Ordovician of Esthonia. Sections were made of some of the specimens identified as *A. mirabile* from Delafield and Iron Ridge, Wis., in the original description of the species, but the internal structure is completely gone and no identification can be made.

ANAPHRAGMA MIRABILE Ulrich and Bassler

Pl. 3, figs. 1-4; pl. 4, figs. 1-4

1904. *Anaphragma mirabile* Ulrich and Bassler, Smithsonian Misc. Coll., vol. 47, No. 1470, p. 49, pl. 13, figs. 9-11.

Material studied.—The cotype suite, U.S.N.M. 43218, from the Richmond group, Wilmington, Ill., includes a sectioned specimen here designated the lectotype, six specimens that are considered conspecific with the lectotype after sectioning, and five specimens of an undescribed species of *Batostoma* that is a close external homeomorph of *A. mirabile* but is quite different internally.

In addition, 21 topotype specimens were studied from the following collections:

U.S.N.M. 2996: Richmond group (approximately 10 feet of beds exposed) on west bank of Kankakee River, just north of U. S. 66A bridge, Wilmington, Illinois. Collected by A. R. Loeblich, Jr.

U.S.N.M. 2997: Richmond group, Wilmington, Illinois. Collected by E. O. Ulrich.

New U.S.N.M. catalog numbers 138273 to 138280 are assigned to individual primary types and topotypes; the lectotype is 138275.

Description.—Zoaria are ramose; branches are generally circular in cross section. Conspecific overgrowth is poorly developed, occurring on three specimens in very thin patches. Monticules are low and difficult to distinguish externally.

In the endozone, zooecial walls range from straight to irregularly undulated and display a considerable variation in thickness. The zooecial walls are laminated and adjacent zooecia are separated by dark zooecial boundaries running down the centers of the walls. These boundaries merge distally into the zooecial boundaries of the early exozone.

In the early exozone as seen in longitudinal sections, zooecial

boundaries are well-defined dark lines or narrow serrated zones and the wall laminae that intersect the boundaries form either a V-shaped or sharply U-shaped pattern. As the walls are followed distally in the early exozone, the V-shaped pattern is generally lost and the U-shaped pattern broadens so that the zone of curved laminae makes up an increasing proportion of total wall thickness. Also, as seen in longitudinal sections, zooecial boundaries are commonly marked by a dark granular zone of appreciable width that can alternate at irregular intervals along a zooecial wall with the more common boundary formed by abutting laminae. As the broadening of the U-shaped laminae progresses distally, the zooecial boundaries become more obscure, until the boundaries are completely lost in later growth stages.

There is a general increase in zooecial wall thickness distally in the early exozone as the zone of curved laminae broadens. Zooecial wall thickness is markedly variable, however, from zoarium to zoarium and also can vary irregularly along the length of a zooecium in the outer part of the exozone. The thickness of a limited segment of a zooecial wall in the outer exozone can decrease to thicknesses common in the early exozone, but the zone of curved laminae remains relatively broad and the zooecial boundary obscure, indicating that wall thickness alone does not determine the nature of the curved laminae and the zooecial boundary. The pattern of laminae is V-shaped and the zooecial boundaries well defined throughout the length of a few zooecia in two of the specimens sectioned.

The general aspect of tangential sections varies considerably with zooecial wall thickness from zoarium to zoarium and also seems to be controlled, at least in part, by stage of ontogenetic development within a zoarium. In the five sections containing exozones of 3 mm. or less in width, the corresponding tangential sections display relatively small acanthopores that cause little or no inflection of zooecial walls, and the zooecial walls range from integrate to broadly amalgamate. In the 10 sections containing exozones ranging from 3 to 5 mm. in width, acanthopores range in size from small, to medium—recognized by noticeable inflection of zooecial walls, to large—recognized by acanthopores controlling cross-sectional shapes of mesopores and zooecia by strongly inflecting their walls. Zooecial walls range from narrowly amalgamate to broadly amalgamate in the 3- to 5-mm. interval. Also within this interval, the three sections showing medium-sized acanthopores are all amalgamate, and the one section that has large acanthopores is broadly amalgamate. In the five sections having exozone widths greater than 5 mm., corresponding tangential sections

all contained large acanthopores and the walls were broadly amalgamate.

Acanthopores are confined to zooecial corners, except in advanced growth stages in which acanthopores are large and have a generally irregular appearance and distribution. Central canals of acanthopores are very small or filled. Mesopores are arranged in an apparently

TABLE 4.—General measurements

	Lectotype	Paratypes and topotypes	
		Minimum	Maximum
Diameter of zoarium.....	6.1	5.4	13.9
Diameter of endozone.....	2.2	2.9	5.3
Average diameter of zooecial void per fragment (longitudinal direction).....	0.27	0.26	0.35
Acanthopores per zooecium	2.7	1.4	4.3
Mesopores per zooecium.....	1.0	0.53	1.6

TABLE 5.—Ontogeny

	Width of exozone	Axial ratio	Tangential aspect
	1.8	0.75	Acanthopores small, zooecial walls integrate to broadly amalgamate
	2.0	—	
	2.5-2.9	0.54-0.65	
	3.1	0.58-0.62	Acanthopores small to large, zooecial walls narrowly amalgamate to broadly amalgamate
	3.8-3.9	0.48-0.54	
Lectotype.....	3.9	0.35	
	4.0-4.4	0.45-0.47	
	4.6	0.46	Acanthopores large, zooecial walls broadly amalgamate
	5.4	0.41	
	5.7	0.35	
	8.1	0.32	
	9.2	0.34	
	9.7	0.26	
	10.6	0.21	

random pattern between zooecia and have walls comparable in structure and nearly comparable in thickness with walls of adjoining zooecia. Some of the smaller mesopores have noticeably thinner walls than adjoining zooecia. No diaphragms were seen in mesopores.

Monticules were not distinguished in all tangential sections, and are generally marked by slight increases in zooecial wall thickness and zooecial and acanthopore diameters.

Quantitative data.—Tables 4 and 5 above are based on sections of fragments from the lectotype and 20 paratype and topotype zoaria. All measurements are in millimeters. The axial ratio is the ratio of the diameter of the endozone to the corresponding branch diameter.

Discussion.—A direct relation exists between the progressive broadening of the U-shaped pattern of the zooecial wall laminae and the amalgamated appearance of the walls in tangential sections. In the early part of the exozone the laminae are V- or sharply U-shaped and the resulting appearance of walls in the tangential view is integrate or narrowly amalgamate. As the zooecia become older and grow distally, the ends of the laminae at the bottom of the U lie in the plane of a tangential section to form the amalgamate band of structureless or granular-appearing skeletal material in the tangential section. Thus, as that U-shaped configuration broadens and takes up an increasing proportion of the wall thickness as the zooid grows older, the amalgamate band becomes broader and shallow tangential sections of older zooecia are broadly amalgamate.

Genus AMPLEXOPORA Ulrich

1882. *Amplexopora* Ulrich, Journ. Cincinnati Soc. Nat. Hist., vol. 5, pt. 1, p. 154; pt. 2, p. 254.
 1890. *Amplexopora* Ulrich, Illinois Geol. Survey, vol. 8, pp. 377, 450.
 1904. *Amplexopora* Ulrich, Ulrich and Bassler, Smithsonian Misc. Coll., vol. 47, No. 1470, p. 41.
 1908. *Amplexopora* Ulrich, Cumings, Indiana Dept. Geol. and Nat. Res., 32d Ann. Rep., p. 739.
 1920. *Acanthotrypella* Vinassa de Regny, Atti Soc. Ital. Sci. Nat., vol. 59, p. 221.
 1935a. *Acanthotrypella* Vinassa de Regny, Bassler, Fossilium catalogus, I: Animalia, pars 67, p. 41. (Considered a junior subjective synonym of *Batostoma*.)

Type species.—*Atactopora septosa* Ulrich, 1879, by subsequent designation herein. E. O. Ulrich published a paper entitled "American Paleozoic Bryozoa" in parts in the Journal of the Cincinnati Society of Natural History. The first part is dated October 1882, the second part December 1882. In part 1, Ulrich established the genus *Amplexopora* with a brief definition (p. 154). In part 2 (p. 254) Ulrich described "*Amplexopora cingulata*, n. gen. et sp. (Plate XI, figs. 5-5b) Generic char., ante p. 154." In remarks following the description of *A. cingulata* Ulrich states, "The species above described I regard as the type of the genus, *Amplexopora*, proposed by me in the last number of the Journal, p. 154."

In part 1, Ulrich preceded his taxonomic section with a discussion of morphology in which he cited four names of species of *Amplexopora*. Two of the names are here considered to have been *nomina nuda*, and two valid, as follows:

One of the *nomina nuda*, "*Amplexopora variabilis*, Ulrich" (1882,

p. 124), has never been validated. The species Ulrich might have been referring to is *Batostoma variabile* Ulrich, 1890.

"*Amplexopora cingulata* Ulrich" is mentioned on page 126 of the October publication but was not described and figured until the December number. Therefore, *A. cingulata* is considered not to have been available as the type species of *Amplexopora*.

One of the two valid species, "*Amplexopora discoidea*, James" (Ulrich, 1882, p. 123), should have been cited as *A. discoidea* (Nicholson). James first listed the name in 1871 without indication, definition, or description. Nicholson borrowed James's types and described them as *Chaetetes discoideus* James (Nicholson, 1874, p. 511, pl. 30, figs. 4-4d) thereby making himself the author of the species. The whereabouts of the primary types is unknown.

"*Amplexopora septosa* Ulrich" is the second valid species mentioned in the October number (p. 128). This citation is in error, lacking the parentheses around the author's name, as the species was originally placed in *Atactopora* (Ulrich, 1879, p. 125). However, Ulrich removed any doubt as to the species referred to by stating that *Atactopora septosa* belonged to *Amplexopora* (1882, pt. 2, p. 255). *Atactopora septosa* Ulrich, 1879, is here designated the type species of *Amplexopora*.

Emended definition.—Zoaria are ramose, frondescent, incrusting, or massive, and monticules are generally well developed. In the exozone, wall structure commonly appears integrate, but can be amalgamate. Laminae from adjacent zooecia intersect a sharply defined zooecial boundary at angles of less than 90 degrees to form a V-shaped pattern pointing distally. Distinct zooecial linings are present in several species. Laminae of the diaphragms are continuous distally with the laminae of these zooecial linings, or in other species, with the zooecial wall laminae. Diaphragms are extremely variable in thickness, curvature, parallelism, and spacing, with compound and cystoidal diaphragms and cystiphragms common in many species.

Mesopores are lacking to few: early chambers are beaded and later diaphragms are regularly and closely spaced. Acanthopores are generally abundant and are of two types: those that are concentrated in zooecial corners and extend throughout the width of the exozone, occurring in all species; and additional acanthopores that are concentrated between zooecial corners and extend through a part of the exozone width, occurring in some species. These additional

acanthopores are generally offset from zooecial boundaries toward zooecial voids causing inflection of zooecial walls.

Discussion.—Based on an examination of thin sections of primary types of species previously assigned to *Amplexopora* now in the U. S. National Museum collections, the following species are considered correctly assigned to that genus:

- A. ampla* Ulrich and Bassler, 1904, Leipers limestone, Upper Ordovician Nashville, Tenn.
- A. cingulata* Ulrich, 1882, Fairmount limestone member of Fairview formation, Upper Ordovician, McKinney's Station, Ky.
- A. columbiana* Ulrich and Bassler, 1904, Leipers limestone, Upper Ordovician, Columbia, Tenn.
- A. convoluta* Bassler, 1935b, Hermitage formation, Middle Ordovician, Harts-ville, Tenn.
- A. cylindracea* Ulrich and Bassler, 1904, Catheys limestone, Middle Ordovician, Nashville, Tenn.
- A. persimilis* Nickles, 1905, Economy member of the Latonia shale, Upper Ordovician, West Covington, Ky.
- A. pustulosa* Ulrich, 1890, Waynesville shale, Upper Ordovician, Hanover, Ohio.
- A. robusta* Ulrich, 1883, Bellevue limestone member of the McMillan formation, Cincinnati, Ohio.
- A. septosa* (Ulrich), 1879, Mount Hope shale member of the Fairview formation, Upper Ordovician, Covington, Ky.

The following species originally placed in the genus *Batostoma* (p. 5) are here reassigned to *Amplexopora*. These species lack the distinctive mesopores of the type species of *Batostoma* and in other characters compare with the type species of *Amplexopora*.

- Batostoma billingsi* Bassler, 1927, English Head and Vaureal formations, Upper Ordovician, Anticosti Island. (Types show mesopores in early exozone that are crowded out in later stages to form typical amplexoporid appearance.)
- B. chapparsi* Loeblich, 1942, Bromide formation, Middle Ordovician, Oklahoma.
- B. conferta* Coryell, 1921, Pierce limestone, Middle Ordovician, Murfreesboro, Tenn.
- B. ? decipiens* Ulrich, 1893, Decorah shale (*Rhinidictya* beds), Middle Ordovician, Minneapolis, Minn.
- B. elongata* Caley, 1936, Wekwemikongsing formation, Upper Ordovician, Manitoulin Island, Ontario.
- B. minnesotense* Ulrich, 1893, Decorah shale (*Rhinidictya* beds), Minneapolis, Minn.
- B. variabile* Ulrich, 1890, top of the Richmond group, Osgood, Indiana. (Type species of *Acanthotrypella* Vinassa de Regny, 1920.)
- B. winchelli* var. *spinulosum* Ulrich, 1893, middle third of Trenton shales, Middle Ordovician, Minneapolis, Minn.

Amplexopora winchelli Ulrich, 1886, from the Decorah shale (*Rhinidictya* beds) Minneapolis, Minn., was reassigned to *Batostoma*

(Ulrich, 1893, p. 295) and is here reassigned to *Amplexopora*, the original genus.

The available evidence strongly indicates that two types of acanthopores are present in the type species and in most of the other Upper Ordovician species of *Amplexopora*. In the type species, the shorter, offset acanthopores generally are concentrated in early and middle parts of exozones and largely between zooecial corners, in contrast to the long acanthopores extending throughout the exozones and centered in zooecial corners. In tangential sections, the total number of acanthopores in areas containing offset acanthopores is approximately twice that of areas without offset acanthopores.

Some of the short offset acanthopores appear almost spinelike. In tangential sections acanthopores are cut transversely and offset acanthopores always have an extension of skeletal material connecting the acanthopores and zooecial walls. Thus, regardless of the first impression given in plate 5, figure 2e, offset acanthopores in three dimensions are not spines supported only at their bases and projecting freely into the zooecial voids, but "spines" supported continuously along their lengths by a ridge of skeletal material connected to zooecial walls.

A distinction is made between inflection of zooecial walls by offset acanthopores and inflection of zooecial walls by acanthopores relatively large in diameter and centered on zooecial boundaries. Examples of inflection by large, centered acanthopores are found in *Amplexopora conferta* (Coryell) and *A. winchelli* var. *spinulosum* (Ulrich), both Middle Ordovician forms.

The taxonomic significance of the offset acanthopores cannot be estimated until much more is known of the distribution of related species and their morphologic variation. Offset acanthopores are not now considered a necessary attribute for the genus *Amplexopora*, or a basis for erection of subgenera within the genus.

The genus *Acanthotrypella* Vinassa de Regny was described merely as a thick-walled *Acanthotrypa* and the originally designated type species is *Batostoma variabile* Ulrich, 1890. The cotypes of *B. variabile* are in the U. S. National Museum collections and consist of four partly silicified specimens from the top of the Richmond group, Osgood, Ind. The cotype originally figured by Ulrich (1890, pl. 35, fig. 5) is here designated the lectotype (U.S.N.M. 43820) and sections are illustrated on plate 7, figure 1. The specimen does not seem to differ significantly from *Amplexopora septosa*, except for the lack of offset acanthopores that inflect zooecial walls. The species is here

placed in *Amplexopora* and *Acanthotrypella* is considered a junior subjective synonym of *Amplexopora*.

AMPLEXOPORA SEPTOSA (Ulrich)

Pl. 5, figs. 1-2; pl. 6, figs. 1-3

1879. *Atactopora septosa* Ulrich, Journ. Cincinnati Soc. Nat. Hist., vol. 2, p. 125, pl. 12, figs. 7-7c.

1882. *Amplexopora septosa* (Ulrich), Journ. Cincinnati Soc. Nat. Hist., vol. 5, pt. 1, p. 128; pt. 2, p. 255.

Material studied.—The cotype suite of *A. septosa*, U.S.N.M. 43621, contained a tangential thin section and a number of unsectioned specimens. After sectioning, seven of the cotypes compared closely with the original thin section and description of the species and are considered to be conspecific. The remainder of those sectioned belong to other genera. The new U.S.N.M. catalog number of the lectotype is 138281; paratypes and topotype are 138282 to 138288. The primary types are from the Mount Hope shale member of the Fairview formation, Maysville group, of the Upper Ordovician at Covington, Ky.

In addition, sections were made from topotype suites, U.S.N.M. 44912 and 44913, collected by E. O. Ulrich.

Description.—Zoaria are ramose; branches are circular to elliptical in cross section. Conspecific overgrowth is common. Monticules are high and nearly conical in outline. The inflection of zooecial walls by acanthopores that characterizes the species can generally be seen on exteriors of well-preserved specimens and seems to occur in randomly arranged groups of zooecia.

In the endozone, zooecial walls are extremely thin and are finely crenulated to nearly straight. Diaphragms are generally sparse and are concentrated in dome-shaped zones extending across the endozones and in the outer regions of the endozones just preceding the exozones.

In the exozone, walls are relatively straight and moderate and constant in thickness for the genus. In a few zooecia, short lengths of wall vary in thickness. Zooecial boundaries in longitudinal view are generally well-defined, dark, serrated lines or zones between abutting laminae from adjacent zooecia. Laminae of adjacent zooecia generally intersect the boundaries at angles much less than 90 degrees to form a V-shaped pattern. A thin zooecial lining is common, and tends to vary proportionally in thickness to the thickness of the diaphragm immediately connected with the lining.

Diaphragms vary considerably from zoarium to zoarium in spacing, parallelism, thickness, and curvature. They range from parallel and widely and evenly spaced to cystoidal, compound, and closely and irregularly spaced. If present, marked thickening or closeness of spacing of a few diaphragms in a zooecium occurs in similar positions in most of the zooecia of a section.

In longitudinal view, the acanthopores that are offset and inflect zooecial walls are visible within zooecial voids for short intervals in areas of the section that happen to be immediately adjacent and running generally parallel to the zooecial walls. The offset acanthopores arise from zooecial walls and are attached to the walls along their entire length by ridges of skeletal material. In thicker sections and polished sections these offset acanthopores appear to vary in length, unlike most acanthopores that are within zooecial walls and run throughout the width of the exozone. The offset acanthopores begin at the inception of the exozone in some zoaria or well within the exozone in other zoaria. The offset acanthopores may end well within the exozone, or may continue to the distal ends of the zooecia. Commonly, the offset acanthopores end at the outermost diaphragm and thus are not seen on the exterior in many areas of a zoarium.

Mesopores are very rare. Early mesopore chambers are beaded. Distally the beading is lost and mesopore diaphragms are thick and closely and regularly spaced. Laminae of diaphragms in mesopores and zooecia are continuous distally with laminae of surrounding walls.

In tangential sections, zooecial walls appear integrate or amalgamate. The amalgamate appearance is generally more pronounced in areas of a thin section that contain offset acanthopores. In zooecia appearing amalgamate in tangential section, the amalgamate band appears granular and its margins merge gradually into the laminated appearance of the inner part of the walls. Zooecial linings are easily distinguishable by a darker shade and sharp contact with the remainder of the zooecial wall.

In areas of tangential sections that do not contain offset acanthopores, acanthopores are dark and are concentrated in zooecial corners. A few occur between corners and are centered on zooecial boundaries. In areas of tangential sections that contain pronounced inflecting of zooecial walls by offset acanthopores, these offset acanthopores are generally between zooecial corners, and the numerical concentration of all acanthopores is nearly twice that of areas without inflection. Offset acanthopores always have an extension of skeletal material connecting the acanthopores and zooecial walls.

TABLE 6.—General measurements (in mm.)

	Original section 43621	Lectotype 138281	Paratypes					
			138282	138283	138284	138285	138286	138287
Diameter of zoarium.....	—	9.5	—	—	7.3	9.1	11.9	7.1
Diameter of endozone.....	—	5.1	—	—	4.1	5.8	9.4	5.3
Average major axis of zooecial void.....	0.21	0.22	0.23	0.20	0.21	0.21	0.21	0.20
Acanthopores per zoecium:								
Zooecial walls inflected.....	5.1	3.9	—	—	3.8	3.3	—	3.8
Walls not inflected.....	—	2.4	1.4	2.2	2.0	1.8	2.2	2.0
Ontogenetic characters:								
No. diaphragms in zoecium.....	—	12	15	12	16	11	6	4
Width of exozone.....	—	4.4	4.1	3.5	3.2	3.3	2.5	1.8
Axial ratio	—	0.54	—	—	0.56	0.64	0.79	0.75

In monticules, zooecia can have enlarged diameters and walls are generally thickened. Monticular mesopores are common and are either randomly or centrally located in the monticules. (See explanation of plate 5 for further discussion of monticules.)

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EXPLANATION OF PLATES

PLATE I

Batostoma implicatum (Nicholson)

- Fig. 1. Longitudinal view of identified specimen, U.S.N.M. 138266, $\times 50$, showing acanthopores with lateral branches or nodes. U.S.N.M. collection 2999.
 Fig. 2. Transverse view of identified specimen, U.S.N.M. 138267, $\times 50$, illustrating the continuity of the zooecial wall of the endozone and the zooecial boundary in the exozone. Note also the typical configuration of the laminae in the exozone. U.S.N.M. collection 2999.
 Fig. 3a. Longitudinal view of identified specimen, U.S.N.M. 138268, $\times 50$, showing several notched acanthopores and continuity between the zooecial-mesopore boundary and the dark, granular, proximal layer of the mesopore diaphragms. U.S.N.M. collection 2995.
 Fig. 3b. Longitudinal view of the overgrowth of same zoarium, $\times 100$, showing wall structure that is typical of the species.
 Fig. 4. Longitudinal view of identified specimen, U.S.N.M. 138269, $\times 5$, showing irregular zooecial growth of anastomosing branches. U.S.N.M. collection 2995.

- Fig. 5. Longitudinal view of identified specimen, U.S.N.M. 138270, $\times 10$, showing configuration of zooecial walls of the endozone. U.S.N.M. collection 2995.

PLATE 2

Batostoma implicatum (Nicholson)

- Fig. 1. Tangential view of identified specimen, U.S.N.M. 138270, $\times 50$, illustrating the passage from the thicker walled growth stage to the younger, thin-walled stage. Note variation in diameters of acanthopores. U.S.N.M. collection 2995.
- Fig. 2. Tangential view of identified specimen, U.S.N.M. 138271, $\times 50$, showing an extreme thickening of zooecial walls and no laminated development of mesopore walls in a relatively young growth stage. U.S.N.M. collection 2994.
- Fig. 3a. Transverse view of identified specimen, U.S.N.M. 138268, $\times 10$, showing transverse shape of zooecia in the endozone and a secondary overgrowth incrusting the primary branch. U.S.N.M. collection 2995.
- Fig. 3b. Tangential view from same zoarium, $\times 50$, illustrating an older growth stage characterized by mesopores largely filled with skeletal material.
- Fig. 3c. Longitudinal view from same zoarium, $\times 50$, showing the thin widely spaced diaphragms of the zooecia, the typical notched acanthopore, and the thick, distally curved diaphragms of the mesopores.
- Fig. 4. Longitudinal view of identified specimen, U.S.N.M. 138272, $\times 50$, illustrating a younger growth stage than that shown in figure 3c. U.S.N.M. collection 2994.

PLATE 3

Anaphragma mirabile Ulrich and Bassler

- Fig. 1. Longitudinal view of topotype, U.S.N.M. 138273, $\times 50$, showing the progressive broadening of the zone of curved laminae and obscuring of the dark, irregular zooecial boundary as growth proceeded from right to left in figure. Distortion into V-shaped laminae in lower zooecial wall is probably caused by proximity of an acanthopore running along zooecial boundary. U.S.N.M. collection 2996.
- Fig. 2. Longitudinal view of paratype, U.S.N.M. 138274, $\times 20$, displaying extremely thin zooecial walls. U.S.N.M. cotype suite 43218.
- Fig. 3a. Deep tangential section of lectotype, U.S.N.M. 138275, $\times 50$, showing a young growth stage in a zoarium with exceptionally thick zooecial and mesopore walls. Note narrowly amalgamate appearance (dark zones between tubes), and small, almost undistinguishable acanthopores in a few zooecial corners. U.S.N.M. cotype suite 43218.
- Fig. 3b. Longitudinal section of lectotype, $\times 20$, showing thick zooecial walls and two diaphragms.
- Fig. 3c. Longitudinal section of lectotype, $\times 50$, showing a diaphragm and dark, granular zooecial boundary zone in middle segment of centered zooecial wall.
- Fig. 4. Longitudinal section of branch of topotype zoarium, U.S.N.M. 138276, $\times 5$, showing thin zooecial walls, and general lack of diaphragms. U.S.N.M. collection 2996.

PLATE 4

Anaphragma mirabile Ulrich and Bassler

- Fig. 1a. Longitudinal section of topotype, U.S.N.M. 138277, $\times 50$, showing moderately thick-walled zooecia that developed broad zones of curved laminae. Note center channel of acanthopore in lower left corner of figure. U.S.N.M. collection 2996.
- Fig. 1b. Longitudinal view from same section, $\times 50$, showing strongly V-shaped laminae and well-defined zooecial boundary in exozone. Note center channels of acanthopores in two zooecial walls at bottom of figure.
- Fig. 2. Tangential section of topotype, U.S.N.M. 138278, $\times 50$, illustrating appearance of advanced growth stages in a thick-walled zoarium. Note the very large acanthopores irregularly inflecting zooecia and mesopores, and the broadly amalgamate appearance of the walls. U.S.N.M. collection 2996.
- Fig. 3a. Deep tangential section of topotype, U.S.N.M. 138279, $\times 50$, illustrating an intermediate growth stage in a thin-walled zoarium. Note the inflection of zooecial walls by the acanthopores and the enlarged zooecium and acanthopore in the monticule in lower right of figure. U.S.N.M. collection 2996.
- Fig. 3b. Longitudinal section of same zoarium, $\times 50$, showing variation in zooecial wall thicknesses and generally U-shaped wall laminae of intermediate and possibly advanced growth stages.
- Fig. 4. Tangential section of topotype, U.S.N.M. 138280, $\times 50$, illustrating young growth stage in a thin-walled zoarium. Note integrate appearance and small acanthopores. U.S.N.M. collection 2996.

PLATE 5

Amplexopora septosa (Ulrich)

- Fig. 1. Transverse view of paratype, U.S.N.M. 138282, $\times 10$, showing transverse shape of zooecial tubes in endozone. Note slight outward displacement of exozone in monticule at extreme left of figure, relative to intermonticular exozone in remainder of view.
- Fig. 2a. Tangential view of lectotype, U.S.N.M. 138281, $\times 30$, showing a monticule with a cluster of mesopores and apparently very few offset acanthopores, surrounded by an intermonticular area containing abundant offset acanthopores. Because of the outward displacement of the exozone in the monticule, the section passes proximal to the zone of offset acanthopores in the monticule, but through the offset acanthopores in the intermonticular area.
- Fig. 2b. Tangential view of lectotype, $\times 50$, showing amalgamate appearance of zooecial walls and offset acanthopores generally concentrated between zooecial corners.
- Fig. 2c. Longitudinal view of lectotype, $\times 50$, illustrating the origin of an offset acanthopore and its spinelike appearance. The apparent distal termination of the acanthopore (distal direction to the right) can be merely the passing of the acanthopore out of the plane of the section.
- Fig. 2d. Shallow tangential section of lectotype, $\times 20$, showing mud-filled living chambers of intermonticular zooecia cut distally to the zone of offset

acanthopores, and monticules in lower right and middle left of figure that are convex enough to project the offset acanthopores into the plane of the section.

Fig. 2e. Longitudinal section of lectotype, $\times 20$, showing a well-developed zonation of offset acanthopores through the middle of the exozone.

PLATE 6

Amplexopora septosa (Ulrich)

Fig. 1a. Longitudinal view of paratype, U.S.N.M. 138284, $\times 100$, showing zooecial wall structure with thin zooecial lining connected directly to the thicker diaphragms. Extreme proximal (left side of figure) diaphragms in both zooecia are compound.

Fig. 1b. Longitudinal view of same specimen, $\times 20$, showing an extreme development of irregularly and closely spaced cystoidal and compound diaphragms. Note offsetting of exozone of monticule in left center of figure.

Fig. 1c. Tangential view of same variant specimen, $\times 50$, showing acanthopores between zooecial corners that cause little offset and inflection of zooecial walls. Other zooecia in the section show the stronger, more typical inflection.

Fig. 2. Longitudinal view of topotype, U.S.N.M. 138288, $\times 50$, showing appearance of a moderate development of offset acanthopores. From topotype suite of U.S.N.M. 44913.

Fig. 3a. Longitudinal view of paratype, U.S.N.M. 138287, $\times 50$, showing a young growth stage indicated by few zooecial diaphragms and mesopore with early chambers beaded.

Fig. 3b. Longitudinal view of same specimen, $\times 100$, showing zooecial wall structure with sharply defined zooecial boundaries of abutting laminae.

Fig. 3c. Tangential view of same specimen, $\times 50$, showing severe inflection of zooecial walls by spinelike acanthopores equal in development to those shown in longitudinal view in plate 5, figure 2c.

PLATE 7

Fig. 1. *Amplexopora variabile* (Ulrich)

Fig. 1a. Longitudinal view of lectotype, U.S.N.M. 43820, $\times 20$, from the top of the Richmond group, Osgood, Ind.

Fig. 1b. Tangential view of same specimen, $\times 20$, showing small acanthopores confined to zooecial corners.

Fig. 2. *Batostoma implicatum* (Nicholson)

Longitudinal view of identified specimen, U.S.N.M. 138269, $\times 50$, showing the appearance of a thin-walled essentially incrusting growth, comparable in dimensions to longitudinal views of *B. ovata*. Note location of incrusting growth in larger view of section, plate 1, figure 4. U.S.N.M. collection 2995.

Fig. 3. *Batostoma ovata* (Ulrich)

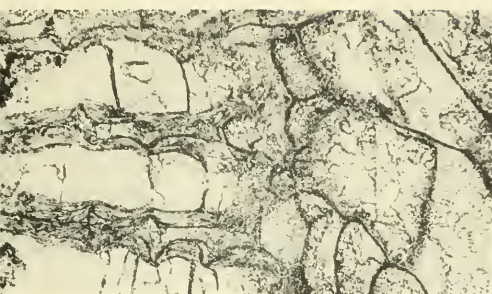
Fig. 3a. Longitudinal view of lectotype, U.S.N.M. 138289, $\times 50$, showing thin, remote zooecial diaphragms, a sharply defined zooecial boundary, and

thicker, convexly curved mesopore diaphragms forming a cystose pattern.

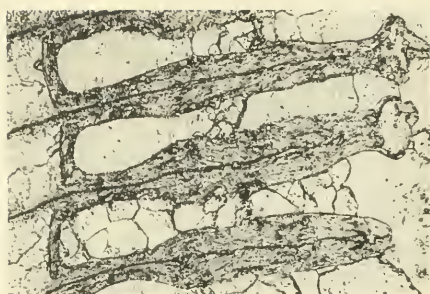
Fig. 3b. Longitudinal view of lectotype, $\times 100$, showing notched acanthopore, typical of those found in most species of *Batostoma*.

Fig. 3c. Tangential section of lectotype, $\times 50$, showing polygonal mesopores, oval, thin-walled zooecia, and acanthopores with structureless cores.

Fig. 4. One of two original longitudinal sections of paratype, $\times 50$, showing convexity of diaphragms in mesopores. U.S.N.M. 43614.



1



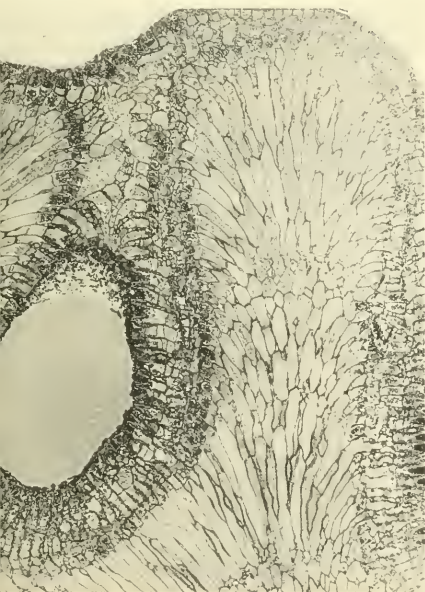
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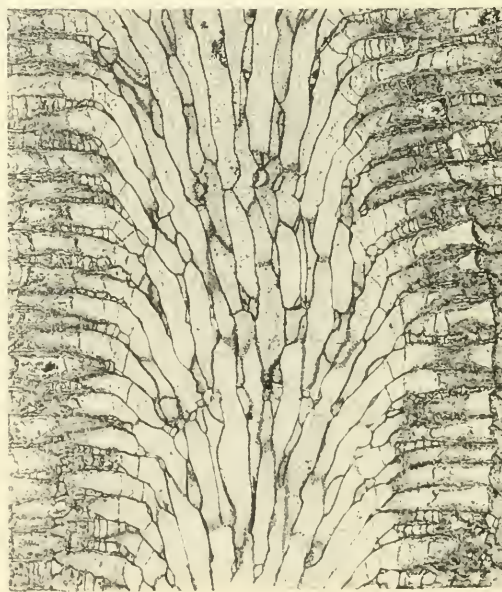
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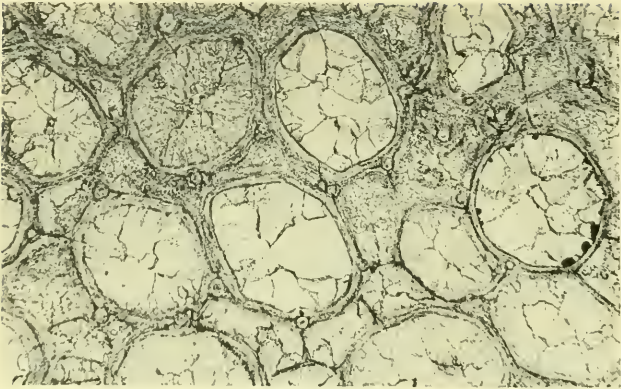
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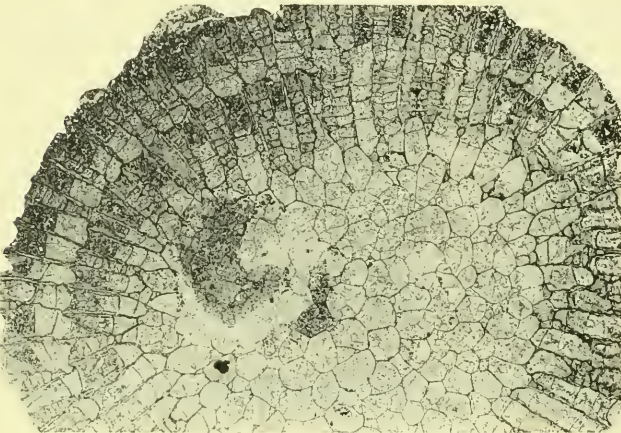
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BATOSTOMA IMPLICATUM (NICHOLSON)

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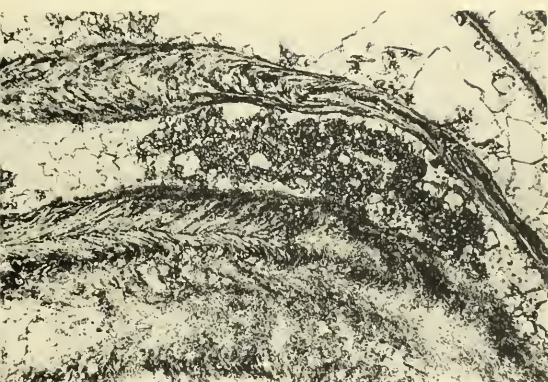
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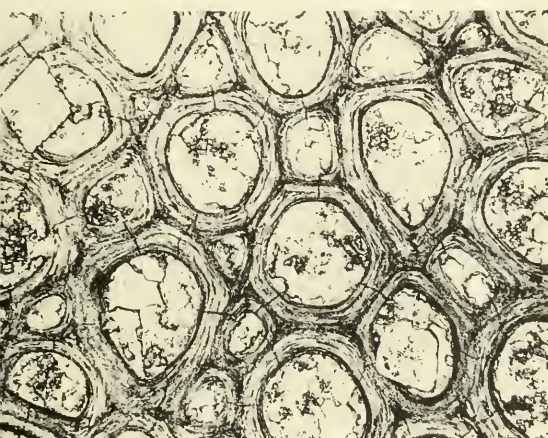
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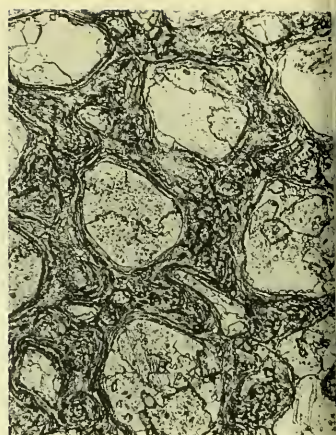
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ANAPHRAGMA MIRABILE ULRICH AND BASSLER

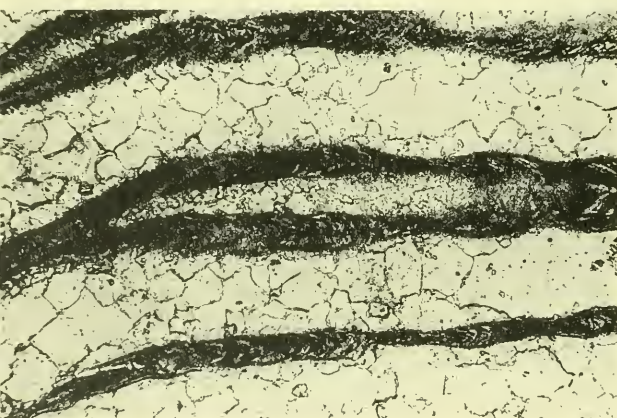
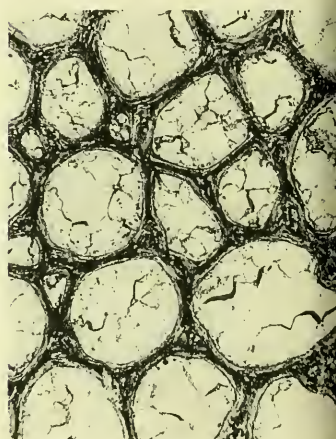
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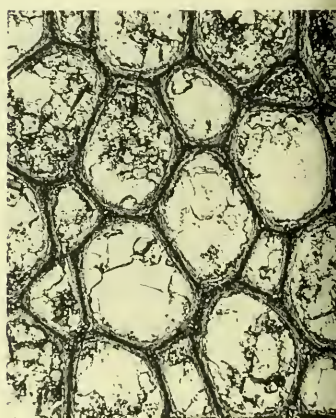
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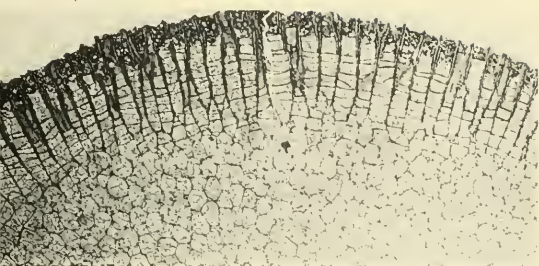


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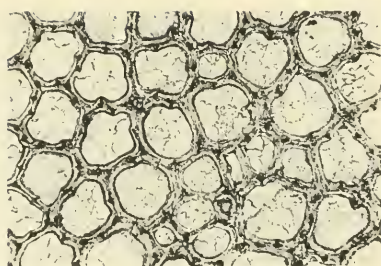


ANAPHRAGMA MIRABILE ULRICH AND BASSLER

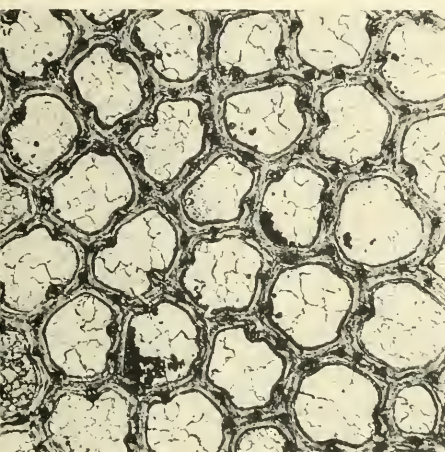
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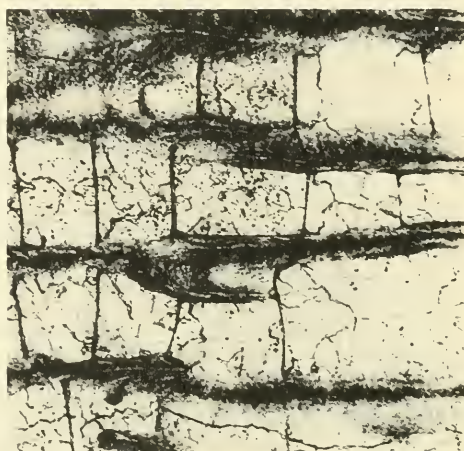
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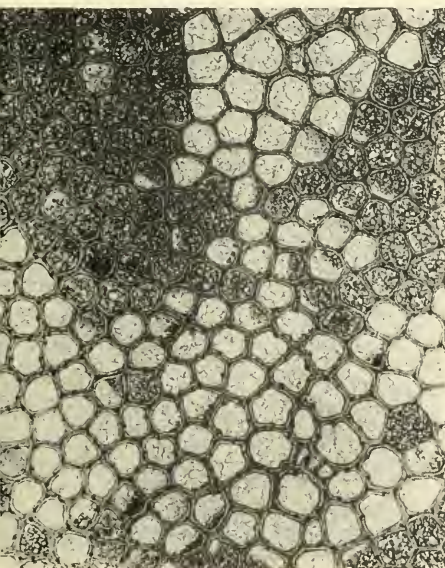
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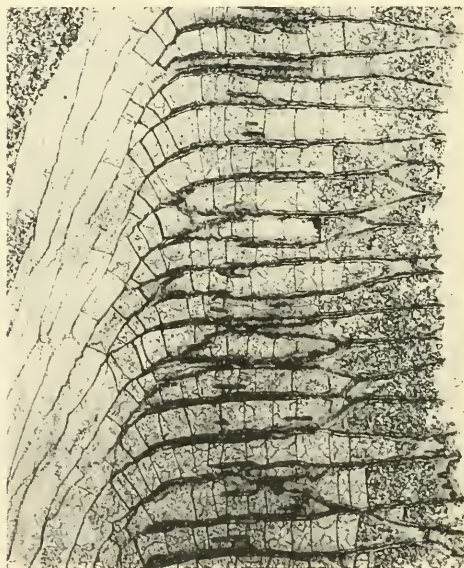
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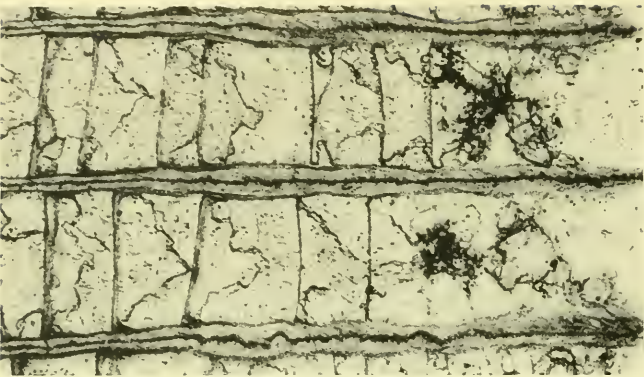
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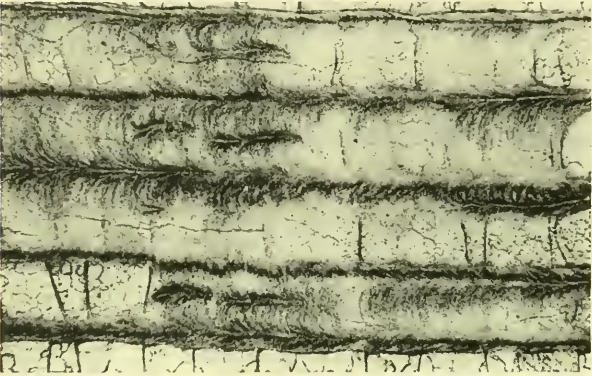
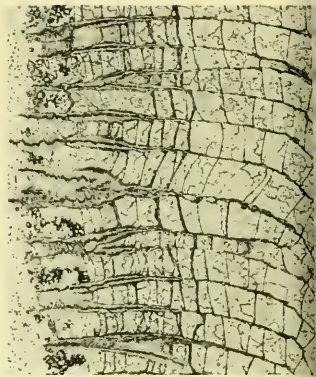
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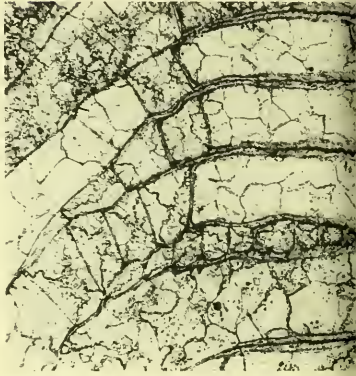
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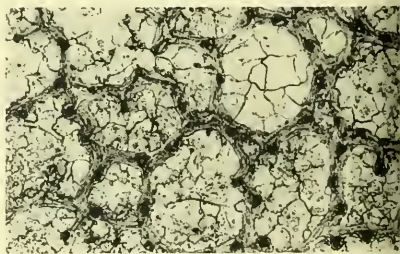
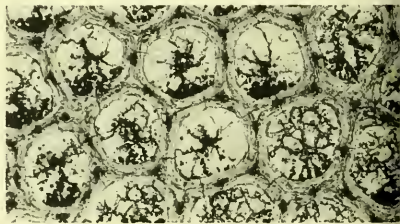
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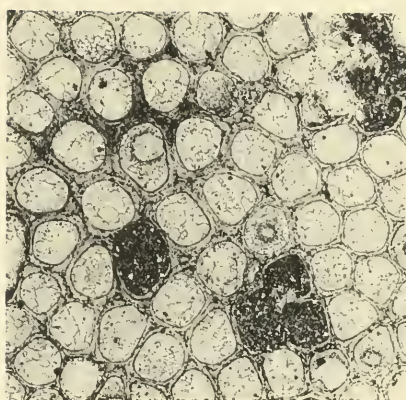


AMPLEXOPORA SEPTOSA (ULRICH)

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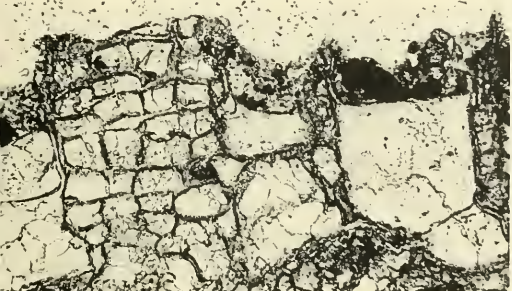
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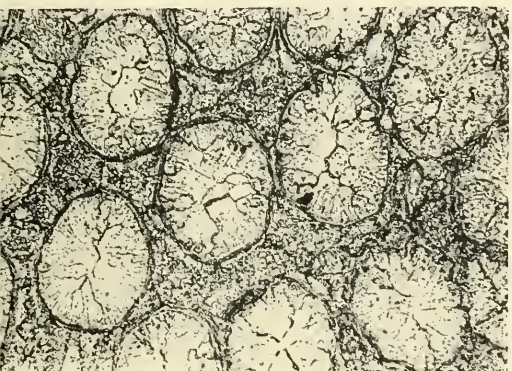
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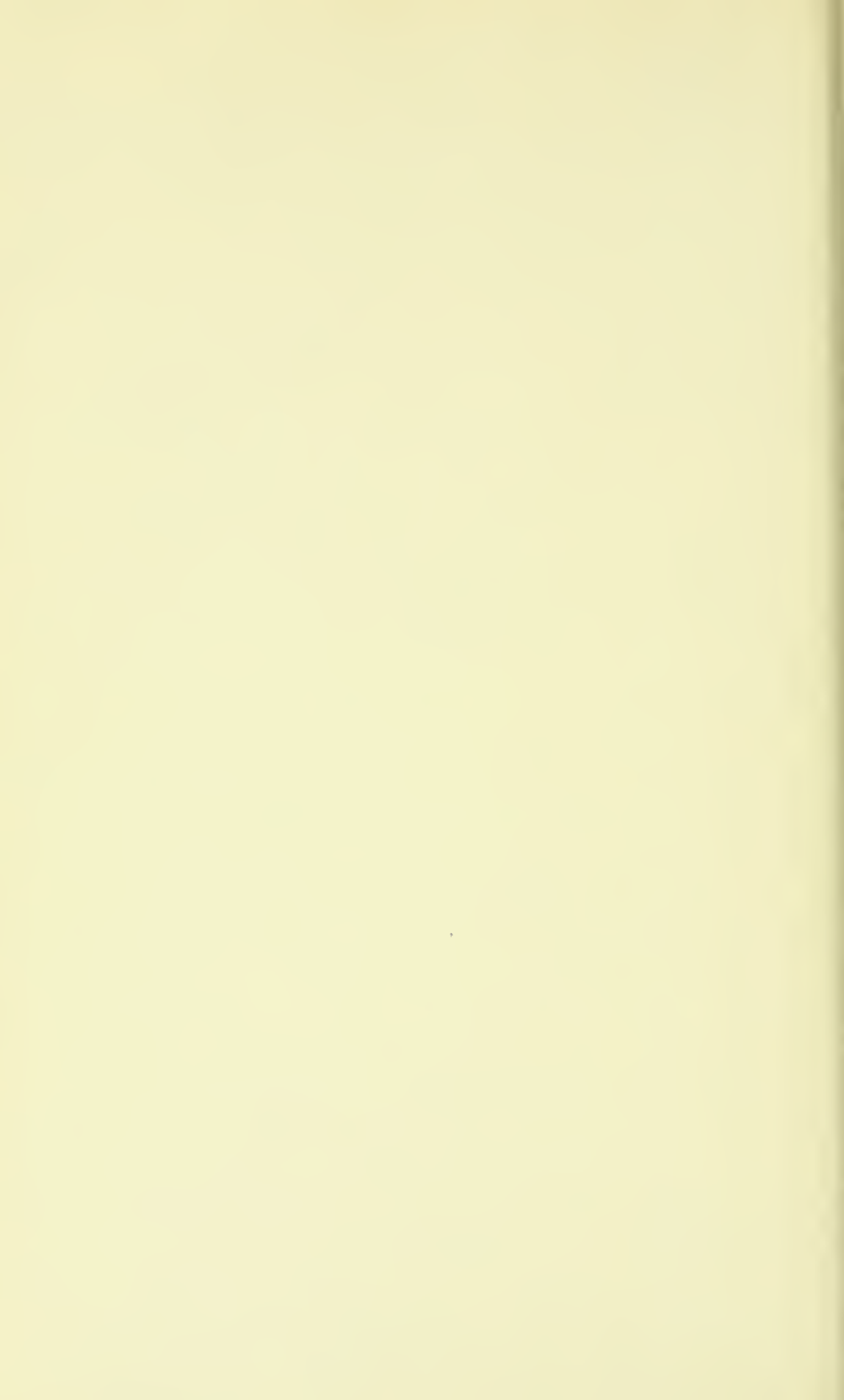


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AMPLEXOPORA MIRABILE (ULRICH), BATOSTOMA IMPLICATUM (NICHOLSON),
B. OVATA (ULRICH)

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